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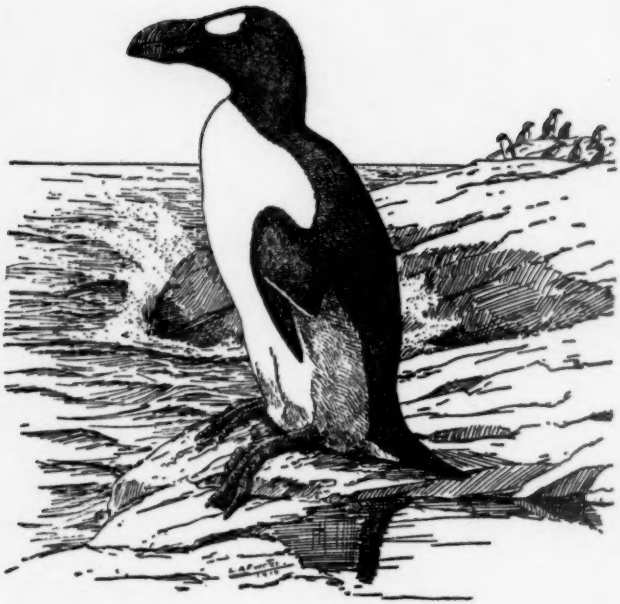

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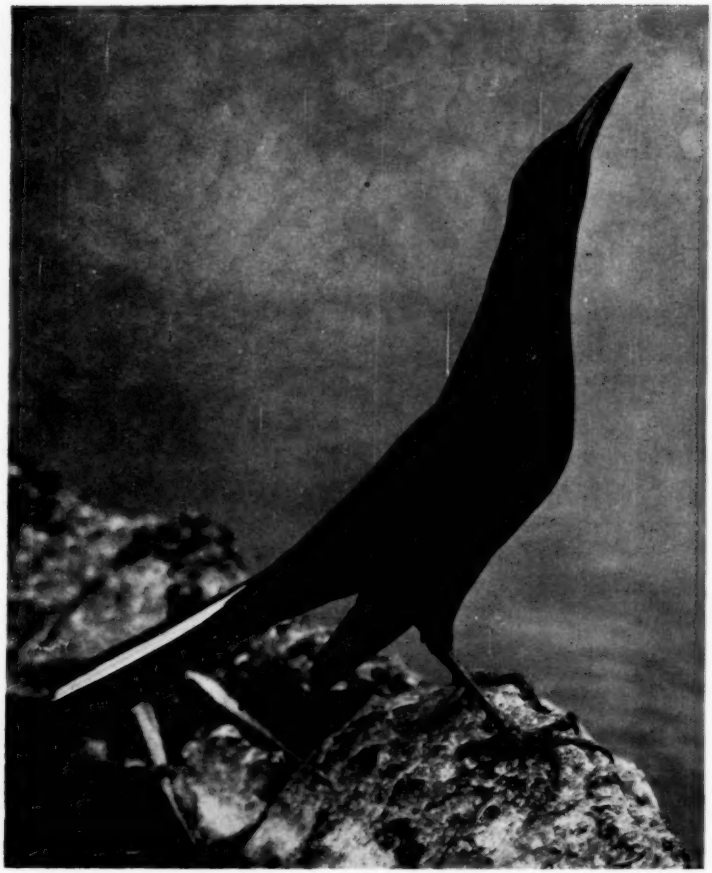

Male Boat-tailed Grackle, *Cassidix mexicanus*, in characteristic display. Photographed by Karl Maslowski at Lake Eola, Orlando, Florida, in mid-January. The white feathers in the tail and elsewhere are abnormal.

The "bill-pointing" or "head-up" display of the Boat-tail so admirably caught by Karl Maslowski's camera was noted by Thomas Belt in a closely related Nicaraguan grackle as long ago as 1874. Identical or similar displays occur also in North American grackles of the genus *Quiscalus*, in Brewer's Blackbird, and in certain cowbirds. Usually interpreted as a phase of courtship behavior, it occurs, in the Bronzed Grackle at least, throughout the year and is used by both sexes. Probably it serves as a warning or threat signal.—Charles F. Walker.

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THE DEVELOPMENT OF SOCIAL BEHAVIOR IN BIRDS

BY N. E. COLLIAS

THE purpose of this brief survey is to illustrate by means of selected examples the manner of operation of factors that control development of social bonds in birds. Socialization of the young individual will be considered first, followed by a discussion of sexual and parental bonds. The general problem of gregariousness and bird flocking is considered by J. T. Emlen, Jr., in another paper (Auk, 69: 160–170, 1952) in this symposium on social behavior in birds.

Each of the different aspects of social development can be analyzed into genetic, physiological, and social levels of organization, and into the interactions between these levels. However, our knowledge of the various factors of social development is still very uneven, and no really general treatment is yet possible. In an attempt at a rounded treatment some unpublished notes of my own will be included.

Much of our more analytical knowledge of the biology of reproduction in birds has been derived, for obvious reasons, from studies on the domestic fowl and the domestic pigeon. At the least, these studies may help to provide guideposts in our search for understanding of wild birds existing in a state of nature, although some wide variations between species may be expected to occur. In the writer's opinion, parallel studies on the behavior of unconfined and undomesticated species of birds have generally shown many more similarities than differences compared to studies on confined or domesticated birds.

SOCIALIZATION OF THE YOUNG BIRD

Social development is one aspect of the development of behavior in general, and as such involves behavior patterns that are laid down prior to hatching; and these in turn depend on the development of structures more directly under genetic control. However, most of the major trends in socialization belong to the post-hatching reactive phase in which activity is generally governed or directed by external

stimuli and is subject to social control. The post-hatching sequence includes certain initial social adjustments, the appearance of new social responses, increasing specificity of social reactions, increasing social independence, and reintegration into new social groups.

Prehatching behavior. Development of behavior depends on and is associated with development of the neuromuscular system, including the establishment of neural connections, the differentiation of enzyme systems, and the establishment of electrochemical rhythms of activity in the central nervous system. Among the very early somatic movements of the chick embryo are simple ventral or lateral twitches of the trunk. Windle and Orr (1934) suggested that these movements were perhaps brought about by the spontaneous discharge of motor neuroblasts, since these authors observed that such movements occurred before the growing sensory nerves had established any central connections in the spinal cord with the motor nerves to the trunk musculature. In the case of certain urodele larvae, Weiss (1941) has found evidence for autonomous activity of fragments of spinal cord placed by this experimenter in the dorsal fin of the larvae. Presumably, endogenous spinal activity is normally under control of the brain.

The development of myelin about nerve fibers in certain brain tracts and peripheral nerves facilitates the functioning of these nerve fibers. Differences in social development between different species may parallel differences in rate of myelinization of the nervous system. In the Starling, *Sturnus vulgaris*, in which the eyes do not open until some days after hatching, and in which the first social activity seems to be the act of gaping (Holzapfel, 1939), the optic nerves are not myelinated until the eighth day after hatching; whereas in the chick of the domestic fowl, *Gallus gallus*, which may open its eyes on hatching, the optic nerve is myelinated six days prior to hatching (Schifferli, 1948). On the other hand, in correspondence with its gaping activities and precociously developed digestive system, myelinization of the hypoglossal and vagus nerves begins earlier in terms of embryonic age in the young Starling than in the chick (*op. cit.*).

Social responsiveness in the newly-hatched chick requires the presence of the basal portions of the cerebral hemispheres, or paleostriata (Collias, 1950a), and this finding emphasizes the importance of studies of the development of the cerebrum in relation to social development. At the time of hatching in the chick, myelinization has proceeded in all parts of the brain, with the exception of the rostral part of the corpus striatum (Schifferli, 1948). In contrast, the young Starling hatches with its brain in a much more embryonic state, with myelinated sheaths present only in the brain stem (*op. cit.*). This species difference in

myelinization of the brain is associated with a marked difference in degree of behavioral and social development at the time of hatching, and may turn out to be a typical difference between nidicolous and nidifugous birds.

There are expansive and restrictive phases to behavioral development. In the chick embryo, movements of the head, trunk, fore limbs, hind limbs, and tail develop on the average in that order (Kuo, 1932). As development proceeds the percentage of independent movements of wing, leg, tail, beak, and eye increases rapidly up to the time when the generalized, active movements of hatching begin (Kuo, 1939). Inspection of Kuo's table (1932:400–405) of the chronology of chick behavior suggests that the development of the prehatching behavior of the chick passes through inactive, active (endogenous), and reactive (responsive to external stimuli) phases.

The extensive studies of Kuo (1932) on the prehatching behavior of the chick, involving about 3,000 eggs, indicate that the basis of social behavior must be laid down in the development of the chick embryo before hatching. Movement responses to touch and pressure generally appear before, but distance receptors for sound and light normally do not function until after, tearing of the egg membranes by the chick in the last few days of incubation. Vocalizations, which are the chief means whereby the newly-hatched chick can emit social signals effective at a distance, appear after the onset of respiratory movements, and usually shortly after the tearing of the egg membranes.

In many respects social development resembles embryonic development. There are many parallels between trends in the physiology of development and trends in social development. As will be brought out in subsequent pages, such principles of embryology as early plasticity, increasing complexity, induction, functional segregation, and functional reintegration of parts resemble the principles of social development.

Initial social adjustments and responses after hatching. Apparently spontaneous movements of the legs, wings, head, and neck during hatching alternate with periods of rest and enable the young chick to hatch. The newly-hatched chick is likely to remain attached to the egg shell by the extra-embryonic membranes for some minutes after hatching; normally it soon pulls loose. Motivation for this activity is indicated by the giving of "contentment" or "pleasure" notes whenever one places traction on these membranes before the chick has broken loose. The normal pulling away tendency of the chick is therefore not entirely an accidental thing. One hen was observed to aid a hatching chick by pecking at the membranes.

Aside from the initial disturbance occasioned by hatching, many young birds at first seem to spend much of their time sleeping.

Spontaneous gaping in young Starlings appeared during the first few hours after being hatched in isolation in a quiet and darkened room (Holzapfel, 1939). Spontaneous gaping tended to disappear in these isolated birds after four or five days, indicating that an inhibitory control had become established, and gaping thereafter appeared in closer relationship to environmental stimuli.

The young of many nidifugous species of birds give characteristic distress calls when isolated from the parent or from the rest of the brood—for example, in young of the: domestic hen, Ring-necked Pheasant, *Phasianus colchicus* (personal obs.); Bob-white Quail, *Colinus virginianus* (Stoddard, 1931); Blue-winged Teal, *Anas discors* (Hochbaum, 1944); Woodcock, *Philohela minor* (Pettingill, 1936); Sandhill Crane, *Grus canadensis* (Walkinshaw, 1949); and European Coot, *Fulica atra* (Alley and Boyd, 1950). In these species the parents have characteristic notes that serve to attract the young. The same reciprocal relationship probably occurs in many other kinds of birds. The young of some nidicolous species may give distress calls; a downy young Marsh Hawk, *Circus cyaneus*, which I placed a few feet from its nest kept up a continual twittering, similar to food-begging notes, while it slowly crawled back to the nest containing the rest of the brood and, having once regained the nest and the company of its nestmates, promptly ceased its vocalizations.

A special study was made of the social behavior of chicks of the domestic fowl. This study was aided by a grant from the Research Committee of the Graduate School of the University of Wisconsin, from funds supplied by the Wisconsin Alumni Research Foundation. The social responses of about 1000 chicks were studied in the course of this work. Only preliminary abstracts have appeared (Collias, 1950a, b), and it seems useful to present some further details here, although more complete data will be published later. I am greatly indebted to my wife, Mrs. Elsie Collias, for her assistance with some of the experiments, and for preparation of the original figures.

These studies clearly show that the distress calls of baby chicks stimulate clucking by a mother hen. The clucking of a broody hen inhibits the distress calls of her chicks and also causes them to emit notes of very different character which, for reasons to be mentioned, are termed "pleasure" notes. Distress calls are loud, insistent peeps which are given repeatedly and carry a considerable distance. Pleasure notes are much lighter peeps of a different quality, are given in much more rapid sequence, and carry only a short distance. The

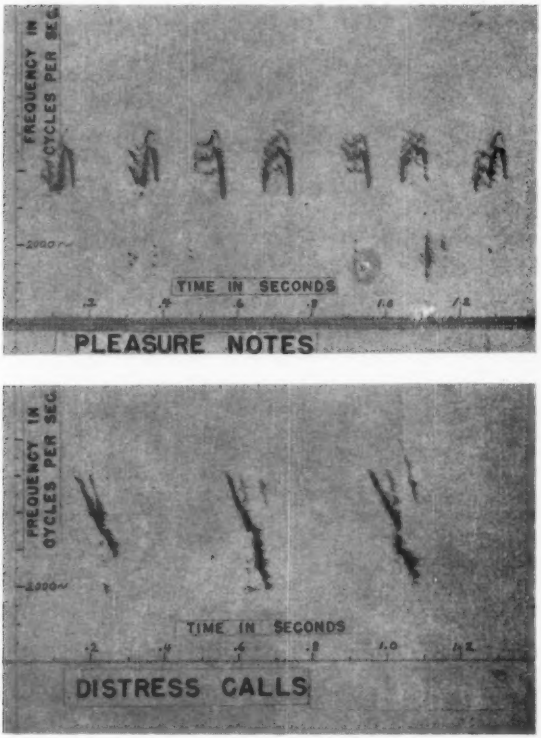

FIGURE 1. Sound spectrograms of pleasure notes (upper) and distress calls (lower) of a chick of the domestic fowl.

sound spectrograms of these two sounds give a precise idea of the energy at each frequency for a given instant of time (Fig. 1). It may be noted from these records that a distress call characteristically differs from a pleasure note in that it is composed of descending frequencies only, and in descending to a lower frequency than that present in any part of a pleasure note. I wish to thank Professor Martin Joos for making these and other spectrograms of the sound signals of the domestic fowl and for aid in the interpretation of these spectrograms.

Upon hatching on a table under direct observation, chicks were found to give their characteristic distress calls apparently because of loss of contact with the eggshell and because of cooling of the moist down. Figure 2 illustrates the initial social responses of chicks within the first five to fifteen minutes after hatching. The two temperature

tests were each taken in the first five minutes after hatching. In the other tests the chicks were tested for successive five-minute periods as represented by the vertical bars, reading from left to right, with the first five minutes post-hatching being represented by the first bar to the left, within each box. At least ten chicks were used for each type of test.

When a chick was hatched under a warm lamp (100° F.) the number of distress calls was very greatly reduced, as compared with a chick allowed to hatch at the subnormal temperature of 78–82° F. If a chick were kept warm and the hand placed over the chick immediately after hatching, few if any distress calls were given.

These social responses can be traced back into the pipped egg. If such an egg be held in the hand and its position changed, presumably shifting the pressure points in the contact of the chick with its shell, the chick inside frequently will give a flurry of pleasure notes. Again, if a pipped egg is alternately cooled and warmed the chick within may sometimes give distress calls or pleasure notes in close correspondence to the temperate changes.

Recently hatched (incubator) chicks paid no apparent attention to mounted specimens of hens. Indeed, a chick placed beneath a mounted hen may desert this foster mother for a warm heating pad placed a few inches away.

Figure 2 shows that positive responses to clucking may be given within 5 to 10 minutes after hatching. Occasionally there is found a pipped egg containing a chick which will respond consistently to clucks by cessation of distress calls. Here again the social response can be traced back into the egg.

If a pipped egg be hold next to the ear, one frequently hears tapping sounds given repeatedly and often at a rate about like that of the normal rate of clucking of a broody hen; these sounds also resemble clucking in their low frequency. These tapping sounds appear to be made by the clapping of the bill, a behavior pattern which Kuo (1932) observed to arise as early as the ninth day of incubation, long before the chick shows any evidence of reaction to external sounds. As mentioned below, repeated tapping sounds usually will quiet the distress calls of recently-hatched chicks. It follows that repetitive sounds of low frequency represent a stimulus situation to which a chick is normally exposed long before hatching.

The response to moving objects developed more slowly than did social responses to other sensory modalities, since it was not evidenced in these tests (Fig. 2) by consistent cessation of distress calls at 5 to 10 minutes after hatching. However, by one hour after hatching,

sight of any object moving near by usually causes a chick to stop its distress calls. Chicks usually open their eyes at the time of hatching, but in the first few hours after hatching they are likely to spend much time resting quietly with eyes closed.

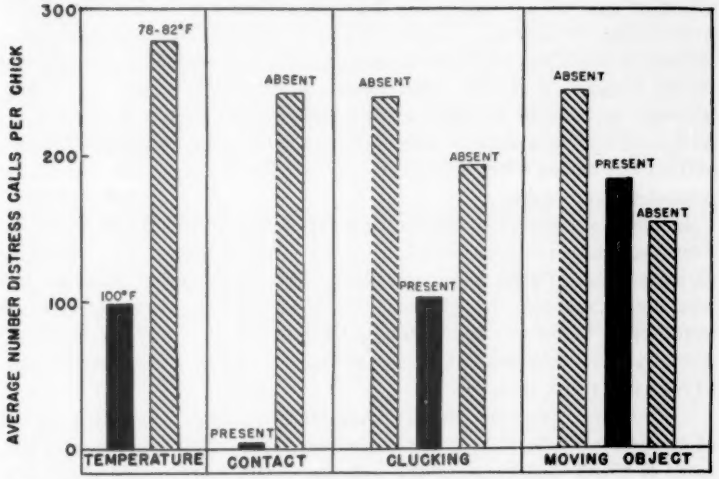

FIGURE 2. Social responses of chicks of the domestic fowl upon hatching in isolation under specified conditions (see text).

The significance of clucking by a hen in the life of baby chicks justified a fuller analysis and account of the properties of this vocalization as a social signal. The initial reactions of each chick were tested separately. An individual chick was removed from the incubator, placed on a lighted table 18 to 24 inches from a loudspeaker connected with a record player, and a record was played to the chick for a definite time interval, during which its responses on initial exposure to a given type of sound were observed through a cheese cloth screen. The degree of approach to the loud-speaker was recorded and notes were taken on vocalizations. As a rule, ten or more chicks in the first three days after hatching were used for each type of test. These tests with phonograph records have shown clucking to have an optimal quality, rate, and loudness. Chicks in the first few days of life respond to wide variations in these sound properties. Interestingly enough, chicks responded well to far greater rates and amplitudes of clucking than are ever given normally by a hen.

Tests with various artificial sounds gave some idea of the response of chicks to different qualitative properties of the sound. Any loud,

harsh sound, such as the warning scream to "aerial predators" of an adult chicken, the scraping of a chair over the floor, a sneeze, or the blaring of an automobile horn, often resulted in escape reactions, *i.e.*, the chick would make an abrupt short run and frequently would hide under or against some object. To repeated hissing sounds the chicks were rather indifferent. To records of a hen clucking, to human imitations of clucking, and even to records of repeated pencil tapping the chicks responded readily with cessation of distress calls, by giving pleasure notes, and by approaching close to the source of the sound. The food call of a broody hen and the low purring sound she uses to attract her chicks when settled in one spot for the night also promptly inhibit distress calls.

In one test series, ten chicks were exposed individually to a specific sound stimulus for one minute, after a minute of isolation to stimulate distress calls. Under these conditions, the frequency of distress calls was decreased 98% by clucking, 85% by clinking two glass bowls together, 65% by an intermittent artificial tone of 256 cycles, and only 25% by the same tone given continuously. All of these sounds were played from disc records.

Very slow or very fast clucking was produced by taking a tape record of the normal rate (1 to 3 per second) and inserting or removing sections of blank tape between the sounds. Chicks responded much better to fast than to slow clucking, but the response slowed down at extremely rapid artificial rates (approximately 10 per sec.).

Loudness of recorded clucking was readily varied by use of the volume amplifier on the record player. Often a chick which was giving repeated distress calls in one spot some little distance from the weak clucking which emanated from the loud speaker abruptly ceased its distress calls and moved toward the loud speaker, as soon as the volume of the clucking was amplified. But extremely loud clucking was less effective, and in chicks a few days old sometimes resulted in escape reactions.

Chicks responded with pleasure notes or cessation of distress calls to very low frequencies of artificial, short, repetitive tones played from disc records, but were generally silent or gave distress calls to high frequency tones (above 400 cycles per second), otherwise similar in pattern. This preference for low tones is correlated with the occurrence of very low frequencies (down to 0 cycles per second) in the clucking of a broody hen, as was revealed by a sound spectrogram of normal clucking (Fig. 3). In contrast, the sound spectrogram of the warning call to hawks as given by a rooster was found to contain only frequencies at or above 400 cycles per second. The prolonged nature

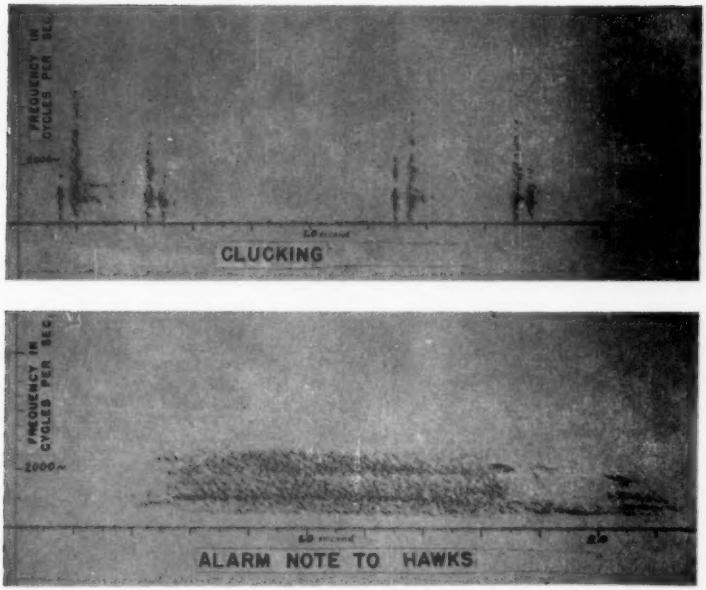

FIGURE 3. Sound spectrograms of the clucking of a domestic hen (upper) and of the alarm cry to an aerial predator as given by a domestic cock (lower).

of the hawk call also seems to be a factor inhibiting pleasure notes. In taking the initial recordings, the "hawk" was merely a piece of cloth thrown up past the cage of the rooster. This simple procedure was found to be very effective for inducing this particular warning cry. The domestic hen gives a warning scream similar to that of the male.

Many of the properties of social responses in baby chicks may conveniently be classified under the same categories used in the analysis of the general properties of the central nervous system. *Latency* is illustrated by the pause of several seconds to several minutes that usually precedes the beginning of distress calls when a chick is isolated. *Rhythmicity* is illustrated by the fact that these distress calls are given repeatedly at fairly regular intervals, showing some tendency to recur in groups. *Fluctuating threshold* is illustrated by the alternation of periods of distress calls with periods of pleasure notes when a chick was kept isolated from its companions for an hour or more (Fig. 4). After preliminary handling this chick was isolated for two hours in a clean cardboard box in a quiet room. In Figure 4 the horizontal line represents the time scale reading from left to right. Vertical lines are each

one minute apart. Vertical lines extending *above* the horizontal line each represent the number of distress calls emitted by the chick for that particular minute. Vertical lines extending *below* the horizontal line each represent the number of five-second intervals in that particular minute during which pleasure notes were emitted; this method of

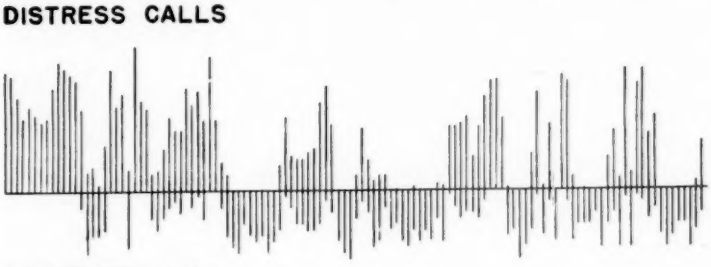

FIGURE 4. Response reversal in a domestic chick isolated for two hours on the day of hatching. Fluctuation between states of "insecurity" and "security" is clearly evident, despite lack of any apparent change in the external stimulus situation (see text).

measurement was adopted because pleasure notes are frequently given at a rate too rapid to be accurately counted without instrumental aid. The actual *reversal of response* secured in this instance suggests oscillation between two balanced neural systems, and is reminiscent of the phenomenon of negative after-image in human visual physiology.

Summation is illustrated by the greater tendency of a chick, which was placed on a table between vertically moving forefingers, to move toward the finger which was allowed to tap the substrate, in contradistinction to the opposite forefinger which was simultaneously moved up and down without permitting it to touch the table. When I alternated the finger that tapped the table the chick would often be induced to run back and forth following sound plus movement versus movement alone. But a baby chick would often go to movement alone, when this was not placed in competition with another stronger stimulus situation. *Afterdischarge* is illustrated by the tendency of chicks which had been petted for a while to continue giving pleasure notes for a few seconds when this contact stimulus was discontinued and the chick was abruptly isolated. *Inhibition* is illustrated by the fact that distress calls and pleasure notes seem to be incompatible—situations that stimulate the one type of vocalization as a rule promptly inhibit the other. Another illustration is the usually prompt inhibi-

tion of all vocalizations by baby chicks when the mother hen gives a warning note. *Specific fatigue* or *refractoriness* may be illustrated by some chicks which stopped giving pleasure notes and sometimes resumed distress calls on long continued exposure to clucking. These chicks were kept under a warm lamp to prevent chilling. The alternation of periods of distress calls with periods of pleasure notes, shown in Figure 4 for an isolated baby chick, could be interpreted as reflecting a corresponding alternation in the state of fatigue, or of an accommodation process, in two balanced and opposing neural systems. Lorenz (1950) has emphasized the importance and extent of occurrence of specific exhaustability of social responses. He observed that repeated elicitation of the "following response" in a hand-raised young Jackdaw, *Corvus monedula*, required progressively greater stimulation. The feeding responses of chicks of the Herring Gull, *Larus argentatus*, can be elicited with cardboard models of the head of the adult, but with repeated stimulation there occurs a steady drop in responsiveness (Tinbergen and Perdeck, 1950).

The characteristic distress calls of baby chicks may be given repeatedly under many conditions of distress that at the same time inhibit pleasure notes: isolation from companions, cold, hunger, thirst, pain, restraint, or approach of a large object. Conversely, the opposite situations as a rule lead to pleasure notes and inhibit distress calls. To some extent, but not completely, at least some of these various stimulus situations can substitute for each other, *e. g.*, a cold chick may cease its distress calls for a short time on being exposed to clucking. The giving of distress calls seems to indicate lowering of the threshold of social responsiveness. Thus, if a baby chick immediately after isolation does not stop its distress calls promptly at sight of an object gently moving near by, it often responds better after it has been isolated and has given its distress calls for a few minutes.

The facts of the preceding paragraphs, taken as a group, suggest the existence of two antithetical neural systems balanced against each other, and corresponding to what in man would be called security-insecurity feelings and responses. This balance provides a delicate mechanism for rapid and adaptive responses to environmental changes.

In general, a chick moves toward stimulus situations that cause it to emit pleasure notes, and away from such situations as bring about distress calls. What a chick does in a complex social situation will evidently depend on the balance of the total external and internal conditions, as expressed objectively in the balance of approach and avoidance tendencies.

We have been dealing in some detail with intitial social responses to an auditory social signal. An excellent example of initial social responses to a *visual* social signal may be drawn from the work of Tinbergen and Perdeck (1950) on the feeding responses of recently-hatched chicks of the Herring Gull. These chicks are not fed until several hours after hatching, and by selecting for testing those chicks that had just dried or were nearly dry these observers believed that a fair proportion of inexperienced chicks was secured. The parent Herring Gull has a red spot on each side of the lower mandible near the tip, and that spot helps stimulate and guide the feeding responses of the chick. By enumerating the relative frequency of pecking responses by the chicks to different types of flat cardboard models of heads of adult Herring Gulls presented in succession under standard controlled conditions, some idea was secured of the stimulus properties of the red spot as a social signal. Absence of this red spot decreased the percentage of positive responses by three-fourths. Color, background contrast, and position of the spot proved important, but differences in color of the bill or head had little or no influence, except that a red bill was somewhat more effective than bills of other colors. A red bill-spot was more effective than any other, including black which has greater contrast value. The importance of contrast was brought out by using a series of models with gray bills and bill-spots of eight different shades of gray ranging between white and black. The percentage of responses increased with the degree of contrast in both directions, *i.e.*, from a gray to a white bill-spot and from a gray to a black bill-spot. The number of responses was decreased three-fourths by shifting the red spot from its normal position near the tip of the bill to a place on the forehead. If the model were held still, responses decreased some 70%, indicating the importance of movement.

Initial social adjustments may involve the development of tolerance for the young by the parents. One broody domestic hen which was incubating eggs at first pecked at chicks placed in front of her, but soon adopted them and ceased to peck at them. I have observed that hens developing broodiness, induced by confining them with baby chicks, at first frequently attack the chicks, then develop tolerance for the chicks, and finally begin to cluck and actively care for the chicks.

The reciprocal nature of parent-young adjustments should be stressed. In a pair of Mourning Doves, *Zenaidura macroura*, which I watched at their nest in a garden in Ohio, the parents took the initiative in feeding the young on the day the young hatched. The parents stimulated the initial feeding responses of the young by pecking gently at the angle of the mouth and particularly by gently pinching the cere

of the young between the parental mandibles. The parents at first inserted the upper mandible, at least, in the beak of the young. On the following and in subsequent days the young helped initiate more of the feedings, and also took a more active rôle by inserting the beak into the mouth of the parent in typical columbiform fashion.

Strengthening of initial responses with social experience. Social attachment quickly increases with social experience in recently-hatched chicks. In the course of routine tests it was noted that at first, responses of chicks to clucking or to sight of a moving object were slow, but after some minutes of repeated exposure a chick responded much more rapidly and over greater distances. At the same time the need for the operative social stimulus was increased, as indicated by much more frequent distress calls between stimulus periods.

Six chicks which I raised by hand until they were ten days of age, when subsequently placed with a broody hen, responded much more slowly or not at all to food-calls of the hen for the first week in her company, as compared to six controls of the same hatch which were placed with the hen on their first day of life and kept with her for the same length of time. The same thing was found in a similar experiment to be true of pheasant chicks placed with a domestic hen. Normally, a broody hen represents to the chick an adaptable complex of attractive stimuli, including warmth, contact, clucking, and movement; and repeated exposure to these stimuli, as well as the food guidance and protection that a hen gives her chicks, helps to strengthen the family bond. At the New York Zoological Park I observed in a pair of Black-footed Penguins, *Spheniscus demersus*, that the parents spent much time preening the head and neck of their young; this probably strengthens the attachment of the young to the parent.

The responses of chicks to each other are part of the family bond and of their socialization. Young chicks of the domestic fowl were very slow to approach one another or failed to come together, even when only five or six inches apart, until after they had experienced some minutes of bodily contact, following which the members of each pair rapidly came together when separated by short distances. This problem was tested with ten pairs of chicks, aged two to three hours, and ten pairs of chicks aged three to four days.

Early social plasticity. Chicks 1, 2, 4, 6, 8, and 10 days of age were tested individually for response on first exposure to clucking. These tests were made in a runway, one foot wide and ten feet long, flanked by cheesecloth walls and with a loud-speaker at either end of the runway, both loud-speakers being connected with a record player. A toggle switch enabled the recorded clucking to be switched back and

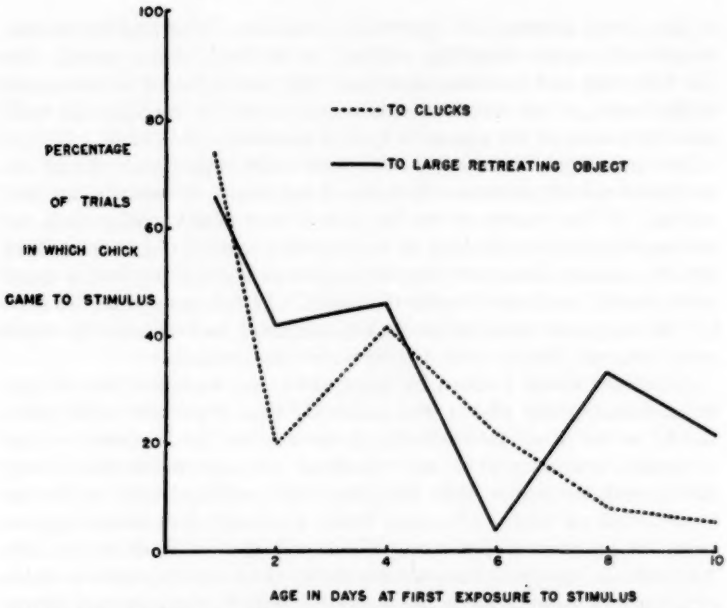

FIGURE 5. Social responsiveness of domestic chicks on initial exposure to a parental object is greatest in the first few days after hatching. See text for explanation of figure.

forth at will from one loud-speaker to the other. Each chick was placed in the center of the runway and was given 10 trials during each of which it was exposed to clucking for one minute. Each trial in which the chick approached to within one foot of the loud-speaker was considered a positive response.

For testing the first responses of these same chicks to a large, retreating object, the observer placed a chick on the floor and then placed himself directly in front of and facing away from the chick. The observer then proceeded slowly away from the chick, often stopping momentarily, or even backing up a few steps, this being continued until about 10 feet had been covered. The usual response of a normal chick in the first few days of life is to follow the observer.

About 100 chicks were given 10 tests, each being tested for response both to clucking and to movements; the results are summarized in Figure 5. The marked decrease in social responsiveness with increasing age is readily evident.

The changing balance of social attraction with fear responses is probably involved in the phenomenon of early social plasticity. In chicks of the domestic fowl, fear responses, such as the tendency to avoid any large approaching object, are very weak on the day of hatching and become stronger by the time the chick is a few days older. The importance of the development of fear responses in relation to early social plasticity has also been indicated in field studies on young Coots by Alley and Boyd (1950).

The younger birds and mammals are, when first taken from their natural parents, the easier they are to tame, *i.e.*, to develop social attachments to human beings. Lorenz (1935) has given a graphic illustration of this phenomenon in Jackdaws. According to Alley and Boyd (1950) young European Coots are wild and difficult to tame after eight hours from the time of hatching. Some species of hand-reared birds may develop social attachments to other species of birds kept in the same room in addition to attachment to the human caretaker (Nice, 1950).

The relative rôles of learning and of more direct genetic control in species attraction vary greatly between different species. Thus, a domestic pigeon reared by Ring Doves, *Streptopelia risoria*, once it matures may continue to associate and try to mate with Ring Doves, rather than with its own species (Craig, 1908; Whitman, 1919). But a Cowbird, *Molothrus ater*, and other parasitic species of birds, normally reared by foster parents, return to their own species for purposes of mating. Birds tend to find and maintain contact with their own species by means of distinctive vocalizations, and the degree to which the song can be modified by abnormal circumstances of rearing seems to vary greatly between different species (Nice, 1943).

Appearance of new social responses. Very young Starlings gape in response to contact, to gentle shaking, to scratching sounds, and to parental vocal signals, but after the eyes open they also gape in response to moving objects. At the same time they become less sensitive to contact stimuli. Orientation responses appear; a young Starling with eyes open at 10 days of age will not follow the pincers with which it is fed, but at 14 days of age it will do so (Holzapfel, 1939).

As a young Robin, *Turdus migratorius*, grows larger it needs more food, and develops louder hunger notes which then seem to indicate a greater degree of hunger for the following reasons. After being fed, the young Robin is silent for a time, then gives light peeps, followed after some minutes by much louder one-syllabled notes, and finally by a series of still louder two-syllabled notes (Fig. 6). A young Robin raised by me in the summer of 1950 and assumed to be two or three

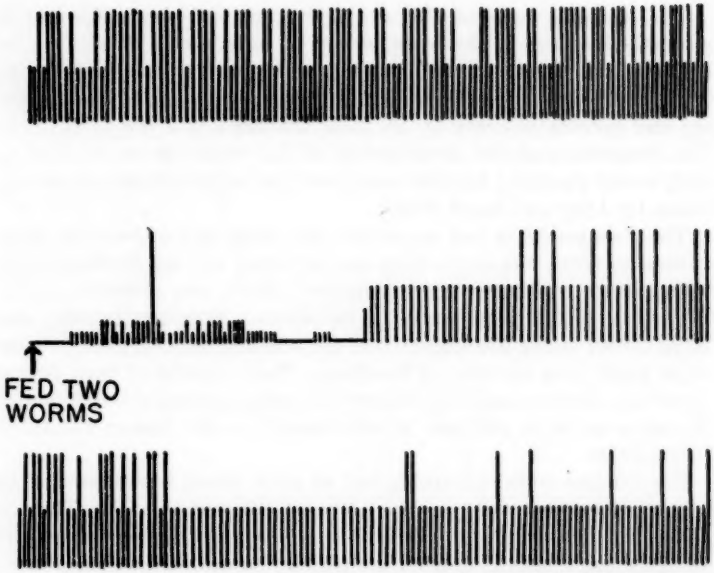

FIGURE 6. Effect of hunger and of feeding on vocalizations by a fledgling Robin. The strength or loudness of each note is indicated by a vertical line, the record proceeding from left to right and from top to bottom; the longest such lines represent loud notes of two syllables and are apparently indicative of greatest hunger. Horizontal lines represent periods of prolonged silence, the period of silence being roughly proportional to the length of the line.

days old when first secured, at first gaped silently and gave the light "hunger" notes after it had been fed; two days later it gave what seemed to be the same notes before being fed, and after some days developed the louder notes, at first the one-syllabled and then the two-syllabled loud call. The latter call appeared at about 11 days of age, assuming the original estimate of age to be correct. Thus the ontogenetic sequence of hunger notes paralleled the same sequence which in the older nestling seemed to reflect the degree of hunger; perhaps this parallelism indicates a gradually increasing development of the internal hunger mechanism. At the same time it is not unlikely that the loud two-syllabled call, which appeared as the latest of the hunger notes, functions to facilitate the parent-young bond in response to the added stress involved when the young bird has left the nest. Figure 7 shows that the loud hunger calls are in all probability hunger-location calls; it could often be observed, as in this instance, that the

young Robin would cease its insistent calling shortly after the caretaker hid himself, only to resume its vocalizations once he reappeared.

Aggressive behavior appears in young birds long after initial responses to the parent. In young passerines pecking at objects replaces gaping. Normally, aggressive behavior makes its first ap-

FIGURE 7. Demonstration that hunger notes of a fledgling Robin could function to inform the parent as to the location of the fledgling. See Figure 6 for explanation of vertical lines. The length of periods of silence is roughly proportional to the space between the vertical lines.

pearance in chicks of the domestic fowl as "play-fighting." Unlike the fights of adult chickens, play-fights do not seem to lead to a definite decision concerning dominance relations. We have observed that as the chicks mature their skirmishes gradually become more "serious," and following a prolonged period of instability a definite dominance hierarchy emerges in the flock. The development of a dominance hierarchy depends on the development of aggressive tendencies in the individual birds of the flock and on their ability to learn each other as individuals.

Sexual and parental behavioral responses may appear in very young birds of some species (Meyer-Holzapfel, 1949). Meyer-Holzapfel suggested that such precocity may be due to the delayed maturation of internal inhibitory mechanisms relative to mechanisms for the sex and parental drives, respectively.

Reproductive behavior is stimulated by the development of pituitary and gonads and of mechanisms responsive to the secretions of these endocrine glands. Birds may differ widely in the time relations concerned. For example, in the Ring Dove and Pigeon the testes do not grow appreciably until two or more months of age. In male chicks of the domestic fowl, growth and secretion in the testes begin within a week of hatching, and by 90 days of age the testis weight has increased some 80 times (Breneman, 1945). At the same time, the difference between these species in testicular growth reflects differences in the pituitary development and differentiation which helps control gonadal growth (Breneman, 1945). This difference in pituitary-gonadal development may prove to be one characteristic difference between nidicolous and nidifugous species of birds.

Increasing specificity of social responses. Following the first appearance of a new social response comes a period of increasing specificity of this response.

This can be illustrated by the development of song from indefinite to definite form in the Song Sparrow, *Melospiza melodia* (Nice, 1943). The first song in this species, as in many other passerines, is an indefinite, nonspecific warble. This is followed by the gradual introduction of short songs, then come longer more adult-type songs separated by greater intervals of quietude but with an undetermined and variable repertoire, and finally adult songs with a relatively fixed repertoire. The degree to which the species song is self-differentiated, or is acquired by hearing other members of the species sing, varies greatly with different passerines. The selective learning by some young passerines of many of the features of the song of their own species deserves critical and extensive investigation.

An increasing social discrimination by young birds is evident when they learn to distinguish different individuals of their species. Craig (1908) noted in families of Ring Doves that the mother becomes unwilling to feed the young long before the father does so, and that the young soon learn to distinguish between their parents, as indicated by their food-begging behavior. The importance of feeding motivation and reinforcement for learning is indicated by the experiments of Holzapfel (1939) on young hand-raised Starlings in which gaping at first occurred in response to a variety of unspecific stimuli; but it finally became restricted to the pincers with which they were fed, or to objects resembling the pincers. Craig also observed that young Ring Doves may at first beg from strange doves, but since the latter refuse to feed them and may even drive them off, the young are familiarized with a further distinction of individuals. Under natural conditions it has been observed that young European Coots will at first follow and beg from any adult Coot, but soon learn to avoid adults in an attitude of attack, and after a while cease to follow or beg except from the parents and avoid strangers without waiting to be attacked (Alley and Boyd, 1950).

The existence of dominance hierarchies within bird flocks indicates that the powers of recognition and discrimination may be extended to many individuals. At a bait station in a marsh during late winter and early spring, we observed a consistent dominance hierarchy among 14 individually marked pheasant hens which regularly visited the corn used as bait (Collias and Taber, 1951).

Cues involved in individual recognition include voice, color, and facial characteristics. Domestic chicks of different broods when

mixed in the dark show some tendency to sort themselves out and go to their own mother, at least when hens of different breeds are used. But some of the chicks may simply go to the nearest hen. In another experiment, I took three well-established broods of chicks from broody hens of three different colors and placed them in the same enclosure with three strange broody hens of the same three colors. The chicks taken from a black mother followed the strange black hen, those taken from a red mother followed the strange red hen, and those taken from a white mother followed the strange white hen. These responses were predominant but not completely exclusive. Schjelderup-Ebbe (1922) observed that alterations in coloration of the face were effective in stimulating attacks on flock mates in a flock of domestic hens. We have observed that changes in coloration of the body plumage or changes in plumage during the molt are quite ineffective in this respect.

Additional evidence of increasing social discrimination is the weakening or lack of social responses by domestic chicks to abnormal stimuli when early social experience has been normal. Craig (1913) stated that young Ring Doves that have never mated are more likely to enter into abnormal matings, as with their own sex, with alien species, or with the hand, or to lay without a nest, as compared with birds which have had mating experience. Young Red-winged Blackbirds, *Agelaius phoeniceus*, just after hatching gape readily to artificial sounds—a hiss, a clap of the hands, or a whistle—as well as to the cluck of the parents, but the response to the artificial sounds disappears in a few days, unlike the response to the parental cluck, which presumably was given more often than the artificial sounds and was reinforced by feeding (Kuhlmann, 1909).

Rôle of leadership in socialization. The strength of the social bond between young and parents is undoubtedly increased by the benefits of the relationship to the young; thus, learning of a diet suitable for a species may be facilitated by parental example, and it functions to reinforce the social bond. Baby chicks will run toward their mother and peck at the spot at which their mother pecks and at her beak. A chick that has never seen lettuce may be very slow in responding to a piece of lettuce placed in its cage, but if one merely taps on this lettuce with one forefinger the chick will run to and peck the lettuce and thereafter eats it with avidity. Movement and the tapping sound are the orienting stimuli here, and eating of the lettuce is the reinforcing stimulus. The parent in many nidifugous species of birds leads the young to a safe roosting spot each evening. Parentless ducklings of the Canvas-back, *Aythya valisineria*, are much less wary than are ducklings still attended by a mother (Hochbaum, 1944:107).

In fact, parent birds furnish guidance to their young in so many phases of life, that they may be said to act in the socialization of young birds somewhat as do special organizers or inductors in embryological development.

The importance of normal parental relations in the life of young birds is suggested in certain game birds by the lesser survival of incubator-hatched, pen-raised birds, as compared to wild-trapped stock, after transplantation, although there are other factors and the matter needs analysis. In one study on banded Ring-necked Pheasants wild-trapped birds showed up to three times the survival rate of game farm birds of comparable age released on the same area at about the same time, mid-summer. Survival was checked during the hunting season in the latter part of November from the percentage of band returns (Harper, Hart, and Shaffer, 1951). According to Studholme (1948) it is practically worthless to release for restocking purposes pheasants under eight weeks of age. However, it seems that young stock is more capable of establishing itself and reverting to the wild than is adult stock, and one study (*op. cit.*) indicated that birds approximately 12 to 14 weeks of age were most suitable for restocking.

In many species of passerine birds the young males normally learn much of the characteristic song of the species from older males of the same species (Nice, 1943). Not all social learning is effected on a parental basis; it may continue during the near-adult period after parental bonds are broken in many passerine species of birds, as in the traditional build up of numbers at a winter feeding station (J. Hickey, pers. comm.). The use of a certain winter roost by Crows, *Corvus brachyrhynchos*, for 50 years or more (Emlen, 1938) is a good example of the effectiveness of older leaders in simplifying what for many birds is a living problem of much importance.

The contagiousness of behavior in domestic chicks facilitates aggregation and socialization. For example, when one chick pecks at the ground its neighbors tend to run over and do likewise. The chicks follow each other as they move along. Some lag more than do others. In 10 groups of chicks, each consisting of 10 to 12 marked individuals which I tested for their response to warmth, each group had one or more individuals which consistently and conspicuously lagged behind the others. These tests were conducted in a narrow runway 10 feet long and 1 foot wide with cheesecloth walls; at each end of the runway there was placed an electric lamp. These lamps provided heat for the chicks which would crowd beneath the lamp that was on. The two lamps were turned on alternately, and when one lamp was turned off the chicks would move to the other lamp which was then on.

Some individuals tended to respond a little sooner than others, and interestingly enough, a few of these leaders would sometimes repeatedly leave the group under the warm lamp and go to the laggard in the cold, which then tended to follow the leader back to the group. From these results it appears that a leader is *less stimulus-bound* than are followers. Such behavior of the leader would be expected to favor survival of the group as a whole.

Increasing social independence. In many species of birds, as the young become older the aggregation tendency is reduced. Thus, a raft of downy young ducklings of the Mallard, *Anas platyrhynchos*, in which the individual young are frequently in physical contact, tends to break up as the ducklings grow, and the individuals are then generally more widely spaced.

Infantile responses may disappear or become latent. Distress calls which are given by domestic chicks on isolation become reduced in frequency as the chicks grow older (Fig. 8). Gaping in young passerines disappears and is replaced by independent feeding responses. In young Starlings raised in the laboratory, pecking began at 20 days, but gaping normally lasted 4 weeks; it was suggested that the overlap in gaping and self-feeding reactions provides a factor of safety during the change to the adult mode of nourishment (Meyer-Holzapfel, 1949). Leaving the nest may in the case of some nidicolous species be facilitated by parental "luring" either with or without food (Nice, 1943:245).

The disappearance of infantile responses may in part be due to cessation of parental care. The disappearance of gaping in young hand-raised Starlings can be greatly accelerated or greatly delayed, by restricting or increasing the amount of hand-feeding, respectively (Holzapfel, 1939).

Regression may appear under stress. It has been observed for a number of species of passerines that young birds in process of learning to feed themselves, when very hungry do not pick up and eat food, but instead start to beg (Nice, 1943:40). The rally call of scattered Bobwhite Quail, according to Stoddard (1931), is merely a modified form of the distress call of the chicks. The biological significance of regression may be that of increasing survival value by rejecting the temporary weakness of the developing individual in favor of the greater survival value of recourse to parental care.

Gradually increasing independence of the young, combined with an increasing indifference of the parents, may lead to breakup of the family. The parent may desert the young as does the female Canvasback (Hochbaum, 1944); young Manx Shearwaters, *Puffinus puffinus*,

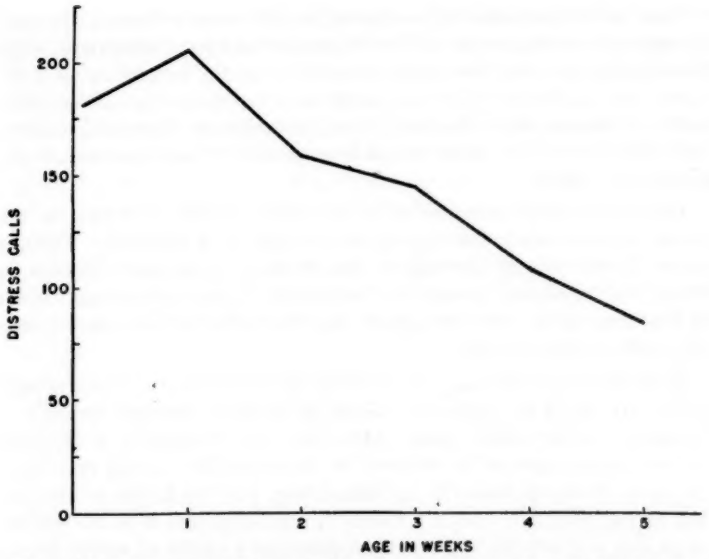

FIGURE 8. Frequency of distress calls by domestic chicks on being isolated changes with age, after the first week. Ten to 17 chicks were tested each week, except that only 6 chicks were tested in the fifth week.

are literally starved out of their nest holes as a result of parental desertion (Lockley, 1942:51).

In some species the parents may even drive off the young at a certain stage, as in the Moor-hen, *Gallinula chloropus* (Howard, 1940). The balance between aggression and parental care may fluctuate during the transitional phase. Howard (*op. cit.*) observed a male Moor-hen chase and peck each young one immediately after feeding it. Song Sparrows drive off their own full-grown young as readily as they drive away strangers (Nice, 1943:253). Loss of parental tolerance for young birds was associated with start of a new nesting season in one pair of Blue Geese, *Chen caerulescens* (Jenkins, 1944). To some extent, rise of aggressiveness, sexual motivation, and exploratory tendencies in the young may contribute to break-up of the family.

Reintegration of the young bird into new social groups. The formation of post-breeding flocks or of breeding pairs or groups requires a certain amount of readjustment, particularly with reference to the balance between cooperative and competitive tendencies of the flock. Species attraction has already been determined by this time, and largely as a

result of socialization within the family (with the exception of parasitic species) the young bird is well acquainted with the habitat, voice, and appearance of its own species.

Increased tolerance for strangers, associated with decreased attachment to the maturing young, may permit the post-breeding combining of families seen in covies of Bob-white Quail by Stoddard (1931) or in flocks of Canada Geese, *Branta canadensis* by Elder and Elder (1949). Previous acquaintance helps determine persistence of subgroups in the flock. When I combined two small flocks of young White Leghorn pullets from two pens into one pen, the two flocks, although often intermixed in the daytime, for months roosted separately at night.

Entrance into a new social group not only requires tolerance of the new individual by the group, but also may be accompanied by the attainment by the newcomer of a definite social status within the group, as has been shown in nature for California Quail, *Lophortyx californica* by Howard and Emlen (1942). For newcomers the initial social status is usually low in the dominance hierarchy.

Social facilitation may aid entrance into new social groups. When two previously acquainted domestic hens are introduced together into a strange flock, the more dominant individual may facilitate rise of its partner in the social scale (Douglis, 1948).

An experienced partner may facilitate formation of a new social bond. According to Levi (1941) young female domestic pigeons placed in a pen with older males will pair more quickly, than if placed with young males.

DEVELOPMENT OF SEXUAL AND PARENTAL BONDS

Just as in human society, the development of appropriate sexual and parental bonds among birds is an integral part of social development in the life history of the individual. The external factors concerned have often been reviewed; emphasis here will be placed on internal factors. The development of sexual and parental bonds is to a considerable extent dependent on changes in the endocrine system, although many non-endocrine factors facilitate or are necessary for the formation of these bonds. Recent literature relating mechanisms of reproductive behavior in birds to hormones has been reviewed elsewhere in some detail (Collias, 1950c) and it will generally not be cited here again, although some of the major concepts will be mentioned.

Sexual bonds. Pair formation involves location of a member of the opposite sex, fighting or threatening away possible rivals, and development of specific tolerance for and attachment to the mate. Location of a mate is facilitated by distinctive vocalizations, generally by the

male, and these special vocalizations are known in many species to decline greatly in frequency once a mate is secured. In a number of species it has been shown that these vocalizations are stimulated by male hormone—for example, the crowing of the domestic rooster, the Ring-necked Pheasant, and the California Quail, the booming of the Prairie Chicken (*Tympanuchus cupido*), the snap-hiss ceremony of the Black-crowned Night Heron (*Nycticorax nycticorax*), the whistle of the Redhead drake (*Aythya americana*), the breeding calls of the male Herring Gull and Laughing Gull (*Larus atricilla*), the bowing coo of the Ring Dove and the Domestic Pigeon, and the song of the Canary (*Serinus canarius*) and the Chaffinch (*Fringilla coelebs*).

Male hormone has also been shown to stimulate aggressive behavior in a variety of birds, including both males and females, although it is possible that a high level of male hormone induces a specific tolerance for females (Collias, 1944). Male Ring-necked Pheasants cease to peck females as the males come into breeding condition (Collias and Taber, 1951). The domestic hen has been proved to secrete female hormone from the cortex of the ovary and male hormone from the medulla of the ovary; female birds in a few other species of diverse types have likewise been demonstrated to be endocrine bisexuals. Therefore, it seems likely that to some extent territorial defense by the females in some species of birds is stimulated by male hormone.

Special displays which may function in sex recognition have been shown to be stimulated by male hormone in the domestic cock, Prairie Chicken, Black-crowned Night Heron, Laughing Gull, Redhead drake, Ring Dove, and Domestic Pigeon. Copulation in the male position has been stimulated by male hormone in the rooster, Ring Dove, and Black-crowned Night Heron. Receptive crouching in the domestic hen is stimulated by female hormone. Pair formation requires hormonal motivation in pigeons at least, since pigeons do not pair if previously castrated or hypophysectomized.

It seems therefore that sex hormones may stimulate the whole complex of sexual behavior, as has been shown most critically for the domestic fowl.

Sexual behavior in birds often involves display of conspicuous features of plumage or of special ornaments, which in many instances have been shown to depend on hormonal control.

Parental bonds. Parental bonds involve attachments to the eggs and young. When eggs are allowed to pile up in breeding pens of Bob-white Quail, some of the birds may start incubating (Stoddard, 1931:459). On the other hand, daily removal of the eggs tends to stimulate laying of an abnormally large number of eggs in this species

as well as in a wide variety of other species of birds. Many species of birds will continue to incubate sterile eggs long past the length of incubation period normal for the species. Broodiness can be induced and maintained for months (as much as six months in one of my hens) in domestic hens by keeping them with baby chicks, but according to Patel's experiments (1936), parental behavior cannot be prolonged in pigeons by giving them a succession of young squabs. Very young chicks are most effective with domestic hens, and as the chicks of a hen grow up and lose their downy plumage the mother shows an increased tendency to peck and drive them from her.

Prolactin secretion induces broodiness in domestic hens, even in the absence of accumulations of eggs or of chicks. In Domestic Pigeons and Ring Doves prolactin induces formation of the crop secretions that are used to nourish the young squabs. In fact, crop growth is a standard, specific, and delicate measure of prolactin secretion.

A certain amount of progress has been made in the analysis of the genetic basis of parental behavior in domestic fowl. In certain breeds of domestic fowl broodiness has been found to depend to some extent on sex-linked factors (Roberts and Card, 1934). According to Hays (1940), broodiness in his strain of Rhode Island Reds depended largely on two pairs of dominant, complementary autosomal genes, with no clear evidence for sex-linkage. Possibly a number of quantitative modifiers are involved. It would seem most probable that in the ancestral type of fowl all these types of genes would be involved.

There is some evidence available on the physiological genetics of broodiness in domestic fowl. The pituitary of non-broody strains of fowl contains less prolactin than does the pituitary of broody strains of fowl (Burrows and Byerly, 1936). Normally, the pituitary of a rooster contains less prolactin and more gonadotrophin than does the pituitary of a broody hen (Burrows and Byerly, 1936). Large doses of prolactin will make a rooster brood and care for chicks (Nalbandov and Card, 1945). Capons may likewise brood and care for chicks; in domestic hens it is known that a high level of sex hormones inhibits broodiness. It is possible therefore that a rooster does not normally brood chicks in part because of differences in the relative amounts of pituitary hormones secreted, as compared to a hen. The Domestic Pigeon belongs to a species in which the male helps to incubate the eggs and feed the young; and in contrast to the situation in domestic fowl large doses of male hormone do not seem to inhibit broodiness.

A difference in response to prolactin is also associated with differences in genetic constitution. Riddle and his co-workers (Riddle and Bates, 1939) found that it was easier to induce broodiness with pro-

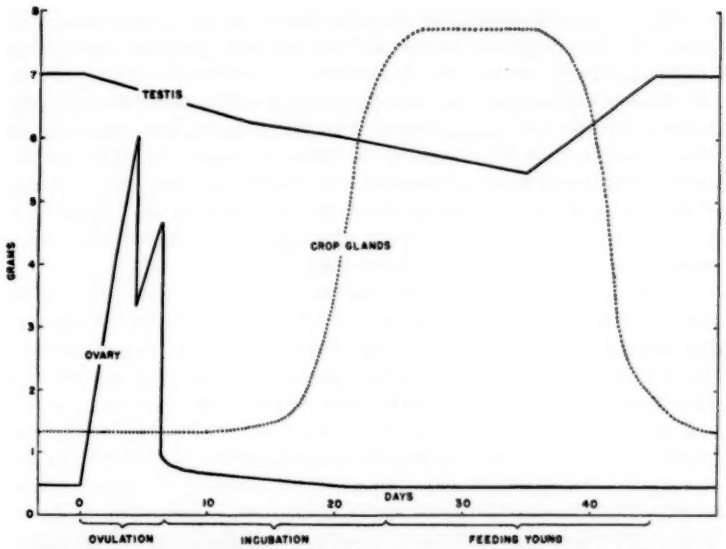

FIGURE 9. The inverse relationship between sexual and parental phases of the breeding cycle in the domestic pigeon. The sexual phase may be measured roughly by changes in gonadal weight. The parental phase may be measured quite specifically by growth of the crop glands (After J. P. Schooley, 1937).

lactin in hens of broody strains than in non-broody strains. Nalbandov and Card (1945) observed that a much larger dose of prolactin was required to induce broodiness in roosters than in hens, and that the amount of prolactin required to induce broodiness in roosters was inversely proportional to the number of genes for broodiness which these roosters were assumed to carry.

Interaction of factors controlling breeding behavior. There is an inverse relationship between the sexual and parental phases of breeding behavior controlled by a parallel inverse relationship in the underlying hormonal changes, as has been demonstrated for the Domestic Pigeon (Fig. 9) and the domestic hen (Collias, 1950c, 1951).

Balanced interaction between hormones of the anterior pituitary and gonadal hormones acts as a basic control mechanism of breeding rhythm in pigeons and Ring Doves. Prolactin secretion in these species is stimulated by secretions from the testis and ovary, but as the level of prolactin rises it inhibits the gonadotrophic output of the pituitary, thereby exerting a strong anti-gonadal effect and reducing its own source of stimulation. Probably a similar mechanism operates

in domestic hens and many other birds. Figure 10 illustrates the case of a domestic hen kept with the same brood of chicks for approximately 120 days. It will be noticed that in this case broodiness and egg-laying, which probably indicate prolactin and gonadotrophic activity of the anterior pituitary, respectively, were inversely related

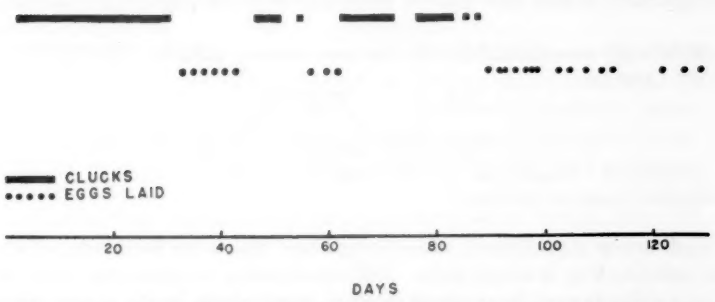

FIGURE 10. The fluctuation or oscillation between the broody phase (indicated by clucking) and the sexual phase (indicated by egg-laying) in one domestic hen, as her chicks grew older and her broodiness gradually disappeared.

and that the hen oscillated between the two phases of reproductive behavior for a time before her broodiness, indicated by clucking, was finally terminated. Such oscillation is characteristic of self-regulatory systems, and reflects the lag in the controlling factors.

Social control of endocrine secretion probably operates through the pituitary gland which is closely related to the central nervous system. The sexual behavior of male Ring Doves increases the rate of ovulation by females, presumably by stimulating the output of pituitary gonadotrophin. Prolactin secretion as indicated by crop growth and secretion can be stimulated in Domestic Pigeons by incubation of the eggs and by sight of the mate incubating the eggs ("psychological brooding"), as has been experimentally demonstrated by Patel (1936). The gonads, by stimulating pair formation, facilitate subsequent development of broody behavior in pigeons. It is possible also that the broody response to prolactin is facilitated by the priming action of sex hormones, as in the domestic fowl.

The occurrence of multiple broods is probably related to a variety of factors. The greater number of broods in the Ring Dove as compared to the Mourning Dove under identical laboratory conditions is associated with seasonal breeding periodicity in the latter species which is more subject to control by changes in day length (Cole, 1933). The Domestic Pigeon is probably relatively unresponsive to artificial

changes in day-length (Levi, 1941) as compared with the domestic fowl; this fact, and the relative inability of young squabs to prolong parental behavior, in contrast to that ability of young chicks, help to explain the greater number of broods in the pigeon.

Figure 11 is a simplified diagram summarizing interactions of some important factors that control breeding cycles in pigeons and doves.

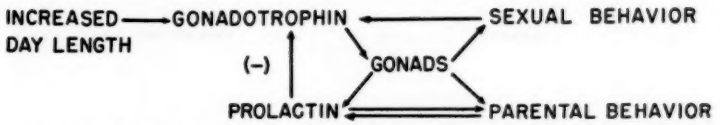

FIGURE 11. Diagram of the interaction of some factors controlling breeding behavior in pigeons and doves.

Each arrow represents a stimulating effect unless an inhibiting effect is indicated by a minus sign. Different species of doves and pigeons may differ in details or quantitatively, particularly in the response to day length. The breeding behavior of the domestic fowl is regulated by a system of factors showing considerable similarity to those operative in pigeons but differing in certain important aspects, as brought out in the preceding pages.

Seasonal adjustment of social bonds. The nature of the factors regulating the seasonal development of breeding and flocking behavior should be mentioned. In this respect the importance of changes in day-length in temperate zones and of wet and dry seasons in the tropics has often been discussed. Social factors generally may play only a secondary rôle; thus, when the Mourning Dove, a seasonal breeder, was mated with the Ring Dove, which at least in captivity is a non-seasonal breeder, seasonal periodicity in egg-laying and fertility of the Mourning Dove under laboratory conditions was maintained (Cole, 1933).

Studies on the annual breeding periodicity of cock Ring-necked Pheasants near Madison, Wisconsin, have shown a general parallelism between changes in day-length, changes in testis-size and pituitary activity, and changes in breeding behavior (Taber, 1949; Collias, 1951). This is a causal sequence with respect to the onset of breeding activity, since it is known for this species that increase in day-length will stimulate testicular activity presumably via the pituitary, and the testicular hormone in turn stimulates breeding behavior in the males.

Little is known as yet concerning the mechanism of the effect of light. Some experiments on immature domestic ducks have indicated that testicular growth may result from very localized light stimulation

restricted to the pituitary gland or to the hypothalamus (Benoit and Kehl, 1939). The hypophysis, unlike the brain and spinal cord, has a special affinity for porphyrins introduced into the body (Klüver, 1944). Porphyrins include some powerful photo-chemicals, and would appear to merit consideration in connection with the problem of the absorption of light energy and its transformation into breeding activity.

Such studies as those of Chapin (1946) on the 9.6-month breeding cycle of the Sooty Terns, *Sterna fuscata*, on Ascension Island (8° S. Lat.) indicate the existence of an internal rhythm of breeding periodicity, and suggest that the ordinary function of changes in day-length is to synchronize and adjust this internal rhythm with seasonal rhythms in the external environment.

Unless habitat conditions are suitable some species of birds may not breed, despite onset of the normal breeding season. In very dry years Gambel's Quail, *Lophortyx gambelii*, of the southwestern United States fail to breed, apparently because of a lack of green food, the growth of which is normally stimulated by rainfall (MacGregor and Inlay, 1951).

It seems to be a general rule that natural selection has so regulated the season of breeding that young birds are generally hatched in the most favorable season for their growth and survival. For example, the peak in numbers of nestlings in Blue Titmice, *Parus caeruleus*, coincides with the peak in numbers of *Cheimatobia* caterpillars that furnish the principal food of the nestlings (Gibb, 1950).

Following the breeding season, the decline in gonadal activity removes an important stimulus to territorial and certain other forms of aggressiveness, thereby facilitating the tolerance that permits flock formation (Emlen and Lorenz, 1942; Collias, 1944).

In summary, the orderly development of social bonds involved in the reproductive behavior of birds depends on the balance and interplay between physical, endocrine, and social factors forming an interacting system that aids ecological adjustment in the sense that it leads to the production of young birds during the season best fitted for their survival.

CONCLUSIONS

1. Social development is part of the development of behavior in general, and as such may be traced back through physiological and chemical levels of organization to genetic factors. What genes determine in this indirect fashion is the tendency to respond to more or less specific social situations; and the interaction between different levels leads to social development.

2. Shifts in physiological balance points, such as those determined by the rate of secretion of specific hormones, play a large rôle in determining the social situation. Thus, sexual and parental phases of the breeding cycle are largely controlled by sex hormones and by prolactin, respectively. In turn, specific social situations react back on and help control the rate of secretion of these hormones. By influencing endocrine secretion, changes in the physical environment may synchronize with internally determined endocrine rhythms in such a way that most breeding activity occurs at the time of year best suited to survival of the young. Flocking of many birds outside the breeding season is associated with the increased tolerance of other individuals that accompanies decline of gonadal activity.

3. The patterning of social behavior parallels the principles of operation of the central nervous system as studied by physiologists, and the development of behavior, including socialization of the young bird, likewise parallels the physiology of development as studied by embryologists.

4. The basis for social reactions is largely developed by the embryo before hatching takes place. The trends in socialization of the young bird after hatching may be summarized as follows: (1) a period of relative inactivity, and sometimes of "spontaneous" or apparently endogenous activity, is followed by (2) the appearance and development of initial, rather generalized, social responses which, passing through an early plastic period, become strengthened, fixated, directed, and specified by social experience. This period of increased social discrimination is followed by (3) a period of gradually increasing social independence that may result in break-up of the family, and finally (4) reintegration into new social groups, a process which in most species of birds seems to be largely governed by the preceding socialization within the family and by the balance between cooperative and competitive tendencies. Social development is greatly facilitated by example and leadership.

5. The results of social development are individuals and groups that respond adaptively to the habitat, habits, and recognition marks of the species, and are therefore ecologically adjusted.

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FLOCKING BEHAVIOR IN BIRDS

BY JOHN T. EMLEN, JR.

MODERN studies of social behavior in birds have concentrated on two problems: 1) the mechanisms of integration of the organized social unit, and 2) the effects of the social environment on the activity, fecundity, and survival of the individual. The first of these has been brought to your attention by Dr. Collias in his discussion of the development of social behavior (Auk, 69: 127–159, 1952). The second will occupy the attention of the two remaining papers in this symposium, those by Dr. Davis and Dr. Darling (Auk, 69: 171–191, 1952). In the interim I would like to bring up for your consideration a third aspect of social behavior—that of flocking responses, gregariousness, and the various factors which determine the size and density characteristics of bird flocks.

The actuality of flocking behavior in birds does not need to be proved. It is everywhere in evidence, indeed it is difficult to find situations and species which do not show at least a trace of it. Large and dense bird flocks are familiar to the most casual observer. Chattering hordes of migrating blackbirds, swirling clouds of swallows in a pre-roosting flight, jostling crowds of sea-birds on a rocky islet; such scenes provide some of the most thrilling spectacles to be seen in bird life.

The term flock, while commonly associated with such spectacular phenomena, will be applied in this discussion to any aggregation of homogeneous individuals, regardless of size or density. The word homogeneous as used here is not to be interpreted in too strict a manner, but is employed in order to exclude the special heterogeneous groupings of sex and age categories occurring in the breeding pair and the parent-young family group. A flock in this broad sense might result simply from a convergence of independent individuals at a common, localized source of attraction such as a patch of shade or a feeding station. It might, on the other hand, arise as a result of a mutual attraction between individuals. In many bird flocks it is probable that both of these factors operate, the relative rôles of each varying with the species and with the circumstances.

SOCIAL FORCES IN BALANCE

The convergence of birds in response to external physical factors presents, in itself, no great problems to the student of bird behavior. Social responses, on the other hand, are highly complex and fraught with challenging problems.

The tendency of birds to respond positively to the presence of others of their kind, commonly referred to as gregariousness, is little understood despite its conspicuousness and widespread occurrence. Various writers have compared it with hunger, a craving or sensation of discomfort which arises in the absence of a physical requirement. Trotter (1916:30) described gregariousness as an impulse in individuals to be in and remain with the flock and to resist anything which tended to separate them from it. Craig (1918) classified it as an appetite, which he defined as "a state of agitation which continues so long as a certain stimulus—is absent," and which is resolved as soon as the appeted stimulus is received. Wheeler (1928:11) compared it with the appetites of hunger and sex and noted its persistent nature and its striking effects on segregated individuals. Various psychologists have regarded it as a condition of responsiveness to social stimuli which, if blocked, leads to frustration activities.

Illustrations of gregarious behavior are not hard to find. Nearly everyone has watched stragglers from a flock of Starlings hurry to join their confreres, or has seen passing Crows respond to a flock of their kind on the ground. Duck and goose hunters are thoroughly familiar with the effect that a group of decoys has on their quarry. Alverdes (1927:108) noted how the artificial isolation of a social animal such as a dog produces numerous signs of discomfort while the presence of a companion, even one belonging to another species, will quiet these "social cravings." Stresemann (1917) discussed the fascination which a flock of birds holds for a segregated individual.

While few would deny this positive social reaction among the members of a flock, Allee (1931) and others have pointed out that there is another factor operating in the formation and regulation of aggregations, the factor of tolerance of social encroachment.

Social tolerance may be considered as promoting flocking behavior by permitting the members of a population to converge in response to either environmental or internal (gregarious) factors. For our purposes, however, it is convenient to consider tolerance in its negative aspect as intolerance, an expression of independence or self-assertion acting in opposition to forces which tend to bring birds together into flocks. Social intolerance is functionally the antithesis of gregariousness. If we follow Craig in calling the craving for companionship an appetite, this second, negative factor is an "aversion," a state of agitation which continues so long as a certain stimulus is present but which ceases when that stimulus is withdrawn (Craig, 1918).

This negative reaction of individuals to crowding is of widespread occurrence in animal populations of all kinds and needs little elabora-

tion. It is particularly conspicuous in birds and is nowhere better illustrated than in the territorial behavior of both colonial and non-colonial species. It underlies most of the situations which lead to conflict between individuals in nature and is considered basic in our modern concepts of the mechanisms of population regulation. Problems of social tolerance and the rôle of aggression in the integration and regulation of bird flocks have recently been reviewed by Collias (1944).

We thus have two opposing forces, a positive force of mutual attraction and a negative force of mutual repulsion, interacting in the formation of bird flocks. The positive force initiates the process and acts centripetally in drawing membership; the negative force serves a regulatory rôle, limiting the size of the flock and preventing close crowding through its centrifugal action. Such a concept may be criticized by those who, encountering difficulties in elucidating emotions in subhuman subjects, object to the word "force" as applied to bird behavior. In the present case, however, I am not referring to any stored or penned-up energy but simply to the cause of the centripetal or centifugal movements observed, whatever that might be (see Webster's unabridged dictionary, 2nd edition, definition No. 15). The responses might be regarded as essentially tropistic and comparable to the prototaxes proposed by Wallin (1927).

No matter what terminology we choose, there seems little doubt that positive and negative social responses occur and interact. Craig observed this interaction in the behavior of his caged Ring Doves as they settled on their roosts for the night. Each bird, he says sought a perch close to friendly companions, *but not too close*, and the difficulties involved in satisfying both the appetite for companionship and the aversion for crowding often kept the birds busy for more than an hour. I have observed similar performances in roosting crows and in loafing flocks of starlings and swallows. By way of illustration, I would like to relate some observations which I made on Cliff Swallows, *Petrochelidon pyrrhonota*, during the past summer.

Cliff Swallows near a group of nesting colonies at Moran, Wyoming, spent much of their time loafing on spans of telephone wires. Positive social forces were immediately apparent in this behavior for the distribution of the birds over the available perches on the roosts was far from random. Of the thousands of linear feet of wire to be found in the area only a few relatively small sections were used at any one time. One or two birds, alighting apparently at random, typically served as the nucleus for a potential gathering. Other birds followed until an aggregation of 100 or more had accumulated, all within a space of 100 to 150 feet.

Negative social forces were also apparent, for in spite of the overall compactness of the group no bird ever held a perch closer than about four inches from its nearest neighbor. Birds were constantly arriving and leaving, and an unstable situation occasionally arose when a bird attempted to secure a perch too close to another, already-settled bird.

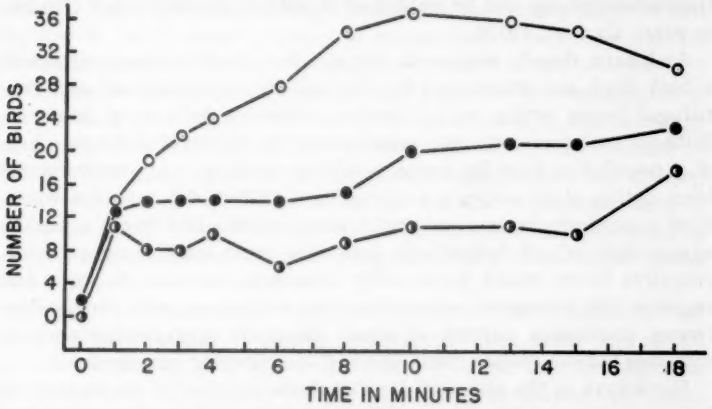

FIGURE 1. Sample curve showing increase in number of Cliff Swallows perching on the central third (open circles), east third (solid circles), and west third (half circles) of a section of telephone wires near Moran, Wyoming, August 4, 1950.

Shuffling and reshuffling inevitably followed until the proper spacing had been reestablished all down the line. Ten-inch gaps were filled centrally and without trouble, a six-inch space on the other hand was usually avoided and, if chosen, was invaded only with the accompaniment of aggressive displays and a local reshuffling of perches. Swallows move their feet but little when once settled and this tolerance limit of four inches may be related to the maximum reach of a bird from a fixed perch.

In an accumulating aggregation of this sort the central portion of the perching area tended to fill more rapidly than did the peripheral portions, and shifts from peripheral to central positions occurred more frequently than did shifts in the other direction. Thus when the perching area was optically divided by the observer into three comparable sections and the number of birds in each of the sections counted at one minute intervals, the central section was seen to grow most rapidly. If the process continued for some time, however, and the central section became filled to capacity, a change in the growth picture ensued and the central section stabilized or even declined while the peripheral sections advanced (Fig. 1).

Observations of territorial defense at the nests indicate that the same narrow but definite tolerance limitations that were seen in the resting flocks on telephone wires applied. The spatial arrangements of nests in the colonies also indicated that the proximity of nest openings was limited by the reach of a perching swallow. Details of these observations will be published shortly in another paper (Emlen, *in press*, Condor, 1952).

As I have already suggested, the size and density characteristics of a bird flock are determined by the balance of centripetal and centrifugal forces acting on an innate pattern of behavioral response. Without such forces we may assume that the dispersal of the members of a population over its range would be random. A positive social force acting alone on such a randomly distributed population would tend to produce clusters and might, if unchecked, lead to the complete aggregation of all individuals into one great and compact flock. Negative forces would presumably intervene, however, to limit and regulate this process of aggregation and, in balance with the positive forces, produce a pattern of small dispersed aggregations each in dynamic balance within itself and with neighboring aggregations.

Variations in the size and density characteristics of flocks may be interpreted as resulting from different balances of these positive and negative social forces. A few species under certain circumstances may exhibit the positive social attraction with very little of the negative element of intolerance. This apparently is the case in the sleeping clusters of tree swifts (Hemiprocnidae), wood swallows (Artamidae), and colies (Coliidae) (Allen, 1925:270; Pycraft, 1910:138). Roosting Passenger Pigeons were said by Kalm (1759) to pile up in heaps on the branches and by Audubon (1831:324) to form solid masses as large as hogsheads. Other examples of clustering occur, particularly among species which roost in cavities, but a far more common situation is to find the birds spaced and jealously defending their immediate surroundings even in large and dense flocks. Thus, swallows space themselves along telephone wires and rarely if ever tolerate physical contact with neighbors. Murres nest in dense colonies yet vigorously defend their immediate surroundings against others of their kind (Howard, 1920:143). Roosting crows, despite early accounts of clustering (Godman, 1842; Wright, 1897:178), characteristically adjust and readjust their perches on the outer twigs of the roosting trees until a suitable interval of three or four inches is achieved (unpublished personal observations made in California and New York).

Small flocks and flocks of low density may be regarded as representing a further shift in the balance through a reduced gregariousness,

an increased intolerance, or a combination of both. Even dispersed social groupings and territorial societies may be included in this concept as cases in which negative forces are strongly developed. Thus territorial Red-wings, *Agelaius phoeniceus*, for all their pugnacity, show many evidences of a colonial social bond (Robert Nero, unpubl. notes). Indeed, as Mr. Darling shows in the concluding paper of this symposium, social attraction may be an essential element of territorial display in relatively dispersed populations of non-colonial species.

The effects of non-social, physical factors of the environment such as a localized center of attraction or a localized source of repulsion may be superimposed on the pattern of dispersal set by the balance of social forces. When such factors are present aggregations may develop which violate the limits of social intolerance and precipitate fighting within the flock. Fighting, for instance, is common at winter feeding stations among species which rarely quarrel back in the brush where food is more generally dispersed.

Artificial confinement or other restrictions to free movement may have a similar effect. Fighting is frequent when birds are placed together in cages, and this is particularly noticeable among non-flocking species (Tompkins, 1933). It is also prevalent in very dense breeding populations of territorial birds where crowding creates the equivalent of spatial restriction (Palmer, 1941:100; Kendeigh, 1941: 42). The increase in aggressiveness which accompanies the spring recrudescence of sexual activity in flocks of California Quail (Sumner, 1935:214) may perhaps reflect a temporary violation of social tolerance resulting from the inertia of the population in adjusting to internal changes in sociality.

With a fluctuating environment such as is encountered in northern and temperate latitudes and a fluctuating physiology such as is characteristic of nearly all birds, the balance of factors determining flocking behavior is obviously far from stable.

The Physiology of Flocking

Having noted the existence of centripetal forces related to social attraction and of centrifugal forces related to social repulsion operating in dynamic balance in bird flocks, it might be profitable to give brief attention to the physiological basis of flocking responses.

Since several forms of social behavior, such as those exhibited in the pairing relationship or in the parent-offspring relationship, are demonstrably stimulated and regulated by specific hormones, one is tempted to search for a hormonal basis for the definite and emotionally expressed social responses. No hormone for gregariousness has been

demonstrated, however. The emotional aspects of social behavior are probably related to nervous tensions arising as a result of frustrated attempts to follow a stereotyped neural pattern of social responsiveness.

Social intolerance, the disruptive element in flocking behavior, is, by contrast, often clearly related to the activity of specific hormones. Male sex hormones have been repeatedly shown to induce birds to fight with their flock associates, apparently as a part of the adjustment for sexual activity. Injections of a male hormone into free living California Quail in winter produced aggressive displays and, within a few days, withdrawal from the flock (Emlen and Lorenz, 1942). Castration, conversely, suppressed aggressiveness and fighting in male pigeons (Carpenter, 1932:522). Such responses in experimental birds suggest that the natural increase in sex hormone secretion by the gonads in spring is directly related to the disintegration of wintering flocks in many species.

Other hormones may influence general aggressiveness under special conditions. Prolactin induces maternal reactions (Riddle, 1935), a form of behavior which involves intolerance of flock associates. Thyroxin has little effect on domestic hens except at high levels when it decreases aggressiveness (Allee, Collias, and Beeman, 1940). Estradiol produces similar effects in hens at high levels (Allee and Collias, 1940).

It thus appears that flocking responses have their physiological basis in stereotyped neural patterns and are influenced by hormonal factors only as these incite disruptive responses associated with sexual or parental activity. The aggregated pattern of distribution, reflecting the unrestricted action of positive social responses of gregariousness may thus be regarded as the neutral or "resting" state, and any deviation from it toward a dispersed pattern, a state of tension effected by the introduction of negative social elements.

Environmental Factors

The fluctuations in sociality which are characteristic of most if not all species of birds correlate with two great rhythms of the environment, the seasonal and the diurnal. In both of these the factors which are associated with increased flocking are those that may be considered unfavorable. This correlation of aggregative tendencies with unfavorable conditions has been noted and emphasized by Alverdes (1927) and various other writers concerned with a wide variety of organisms, both vertebrate and invertebrate. Such

generalizations should be extended with caution, however, for they may tend to hide the true relationships.

Seasonal factors fluctuate at a slower tempo than diurnal factors, and their effects may thus become integrated with the slower forms of response mechanisms in the bird's physiology, such as those which involve conspicuous morphological changes of the primary, secondary, and accessory sexual structures. Diurnal factors, on the other hand, fluctuate at a tempo which precludes major morphological adjustments, and behavioral fluctuations associated with them are more superficial.

Two factors associated with the seasonal cycle which commonly promote flocking are low temperature and low precipitation. These correlations may be seen in the normal seasonal activity cycles of many birds but are best illustrated, freed from the possible effects of innate rhythms, in the behavioral responses of local populations to irregular fluctuations of weather.

Although the spring recrudescence of sexual activity with its corollary aggressiveness is basically a physiological response to increased day-length, cold temperatures have a profound modifying influence. Red-winged Blackbirds, for instance, respond to a cold spell during early stages of the nesting cycle by abandoning their aggressively defended territories and returning to a winter flocking behavior (Beer and Tibbitts, 1950:63). Many other species behave similarly. Flocking should not be regarded as a general response to cold, however, for in those species which habitually breed in flocks, the effect of cold may be quite different. Thus Cliff Swallows in several colonies near Moran, Wyoming, in 1950 responded to an unseasonable cold spell early in the nesting season by temporarily abandoning their half-built nests and shifting for two days from one type of flocking behavior at the nesting site to another, slightly more dispersed type on foraging grounds several miles away (Emlen, *in press*, Condor, 1952).

Drought is another environmental factor which, occurring abnormally, may promote flocking responses during the non-flocking season. This has been noted in Gambel Quail, *Lophortyx gambelii*, in arid portions of southern California and Arizona where a failure of the usual spring rains inhibits the normal spring dispersal of the winter coveys (Leopold, 1936:28). Endocrine disturbances resulting from nutritional deficiencies are thought to be responsible (MacGregor and Inlay, 1951).

It thus appears that the behavioral responses of birds to unseasonable cold or drought constitute essentially a return to the non-breeding pattern of the species. This implies a suppression of sexual activity

and suggests a reduction either of hormone output or of responsiveness to persisting levels of hormone in the blood. Regardless of the mechanisms, however, we may conclude that unfavorable weather promotes flocking behavior by suppressing the disruptive element of social intolerance. There is no evidence that it directly modifies gregariousness itself.

Light intensity is the principal environmental variable of the diurnal cycle, and it is quite evident through observations of roosting behavior that darkness is associated with increased flocking in a great many species. One has only to recall the great roosting assemblages of such diverse birds as herons, gulls, vultures, pheasants, pigeons, swifts, crows, swallows, blackbirds, and robins to capture a realization of this response to the light cycle.

Such sudden fluctuations in sociality are probably not associated with hormonal changes such as those involved in the seasonal cycle; at least no such relationships have been demonstrated. Perhaps they can best be explained by relating them to the schedule of general activity imposed on the birds by alternating periods of light and dark. Night is a period of enforced inactivity for most birds, while the hours of daylight provide the only time during which foraging and other essential activities of self-maintenance can be performed. Self-maintenance calls for independent action which, while not necessarily involving social intolerance, entails a certain amount of freedom from interference. Thus, the members of a covey of quail disperse slightly from their compact roosting aggregation during the morning foraging period, may reunite to loaf during the noon hours, and then fan out again for a second feeding period before finally congregating for the night. The spectacular flights of blackbirds to and from their huge roosting assemblages reflect the same alternation of periods of activity and rest in a pattern and on a scale compatible with their special feeding habits and greater mobility. The limited acreage of a blackbird roosting-site could not conceivably support, even briefly, the hundreds of thousands of birds which congregate on it nightly.

Thus, after foraging in a relatively dispersed pattern, and in a relatively independent manner during the day, the members of a population are temporarily released from the demands of self-maintenance and are permitted to respond freely to their basic gregarious appetites.

RESUMÉ AND CONCLUSION

Symposia such as the present one provide perhaps a legitimate excuse for a little speculation. I hope that I have not abused this privilege and stepped too far beyond the firm shore of established facts.

My objective has been to develop a theoretical basis for interpreting flocking behavior and the various factors, both internal and external, which affect it. For this I have proposed that the form and density characteristics of bird flocks are determined by the interplay of positive and negative forces associated with gregariousness on the one hand and intolerance and independence on the other. Gregariousness has its basis in stereotyped neural patterns, and there is no evidence at present that it is affected directly by hormonal or environmental influences. Social intolerance and independence, on the other hand, are highly variable, and in their variations regulate and determine the dispersal or flocking pattern of the population. Flocking reaches its highest development when gregariousness is given free rein, unrestricted by conflicting demands of reproduction and self-maintenance.

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SOCIAL BEHAVIOR AND REPRODUCTION

BY DAVID E. DAVIS

THE subject of social behavior and reproduction requires delimitation in order to clarify the scope of this part of the symposium (see Auk, 69: 127–191, 1952, for other parts of the symposium). In its broadest sense social behavior apparently includes any behavior between or among individuals of a species. However, for this paper the term will be restricted to the aspects of social behavior that influence the reproduction of the species as a population. This is a rather functional viewpoint because it considers the results of the behavior in terms of reproductive success or failure. It seems obvious that social behavior has relations with reproduction in birds because insemination is necessary in all known species of birds. The act of copulation is of course a form of social behavior. However, this does not settle the problem, because birds have developed a bewildering complexity of behavior patterns associated with reproduction. Our task is to obtain an understanding of the extent of causal relation between social behavior and reproduction.

The general thesis to be developed is that a large proportion of the social behavior assures or at least increases the success of reproduction. This thesis is rather difficult to test because, obviously, those species that lacked the social behaviors that assured reproductive success are no longer present. Thus we must deduce that, because of the absence of these behavior patterns, the species vanished. This type of evidence is unsatisfactory from the experimental viewpoint. Furthermore, as will be described later, the detection of the factor that limits a population is very complex.

The discussion will be divided into three major parts: 1) Courtship behavior clearly influences the production of eggs and the raising of young; 2) Territorial behavior affects the supply of environmental requirements; and 3) Hierarchial behavior is another method of regulating the utilization of resources. These three aspects affect reproduction in somewhat different manners.

COURTSHIP AND THE NESTING CYCLE

Courtship behavior in general seems to ensure that, at the appropriate times, a mate will be available to fertilize the eggs and assist in the work of raising the young. Some species require two individuals for most of the reproductive cycle in order to breed successfully, while other species get along with the barest minimum of collaboration.

An example of the minimum is provided by Gould's Manakin, *Manacus vitellinus* (Chapman, 1935). This species is a rather primitive passerine bird living in the jungles of Central America. Several males of Gould's Manakins make courts in the underbrush of the jungle. Each bird clears all leaves and twigs from the ground and establishes a perch above the bare area. The males display toward one another by means of "bluffing," and especially by snapping the wings together behind the back, producing a sharp noise. The dull green female, as she approaches sexual readiness, tends to remain near the court. When she is ready she enters the court of one male and with him performs a fantastic mutual dance consisting of leaping in the air and passing over each other rhythmically. After a short period of dancing the birds disappear into the woods, presumably for copulation. The male returns to his court and the female completes the nesting activities alone.

This type of mating is found in other species. The Tailed Manakin, *Chiroxiphia caudata*, of Brazil performs a similar dance, although I have never seen more than three individuals at one spot. The birds do not clear the ground beneath the dancing area and are able to make only minor noises with their wings. Wagner (1945) describes the courtship dances of the closely related *Chiroxiphia linearis* of Mexico. This species clears the ground under the dancing area.

There are, of course, many other examples of species that meet for only a brief period of time to copulate. Some of the best known are the Ruff, *Philomachus pugnax*, and the Sage Grouse, *Centrocercus urophasianus*. These species differ in the details of their courtship behavior and reproductive patterns, but all appear to reproduce adequately to maintain the species. For example, the manakins as a group are definitely successful in South America. Many of the others are clearly thriving species.

Another group of species utilizes the courtship ceremonies to maintain the sexual bond for the period of building the nest and, in many cases, the entire nesting cycle. The nuptial bond is of course formed at or sometimes before copulation and in many species is maintained for a period beyond fertilization. Most passerine birds maintain courtship ceremonies during nest-building and beyond. Ducks, however, show a transitional phase. The birds pair on the wintering grounds (Hochbaum, 1944) and remain together until the nest is built and the incubation has started. No example comes to mind of a species in which the male helps to build the nest and then deserts the female. We can postulate that such a stage in the evolution of behavior probably existed, but that it disappeared due to the continuation of the mutual bond to almost the end of the nesting cycle.

In some species the male is the chief architect of the nest. The male House Wren, *Troglodytes aëdon*, constructs the major part of the nest before copulation and may, under some circumstances (Kendeigh, 1941), prepare several nests and be polygynous. A somewhat similar behavior occurs in the Baya Weaver Finch, *Ploceus philippinus*, (Ali, 1930) in which the number of females obtained by a male depends upon how many nests he can build. In these cases courtship hardly functions to provide the necessary structure for reproduction but does maintain the function of arranging a suitable meeting of the two birds.

Some more primitive species maintain elaborate courtship performances that appear to be related to the proper maintenance of incubation. Doves of many species share the incubation between the sexes and continue elaborate ritual during this time. Black-crowned Night Herons, *Nycticorax nycticorax* (Allen and Mangels, 1940) not only maintain courtship ceremonies but develop elaborate performances when the mates exchange incubation duties on the nest. The performances involve plume erection, bill-rattling, and weak call notes. It is perhaps significant that both sexes incubate in a large number of species that feed far from the nest. This may be assumed to be an adaptation for protecting and warming the eggs while one parent is absent for a long period of time. Thus species are able to utilize a distant source of food by developing incubation behavior in both sexes. The social behavior patterns of courtship maintain the members of the pair together, and the ceremonies at the nest permit a harmonious exchange of incubation duties.

The argument can be extended to the problem of feeding the young in the nest. To supply an adequate quantity of food for the young requires strenuous efforts by the parents. Presumably the activities of both adults of some species are necessary to keep the young fed. Thus the result of courtship performances is that the pair is maintained through the period of feeding young. Examples readily come to mind. The male Song Sparrow, *Melospiza melodia* (Nice, 1943:171) assists regularly in feeding the young even after they have left the nest. The male House Wren (Kendeigh, 1941), however, may begin another nesting cycle before the young have left the nest. It may be assumed, since both species reproduce at a rate adequate to maintain a population, that differences in the availability of food permit this slight difference in behavior.

Since the young soon learn to take care of themselves there is little need for the parents to continue their bonds for this function. However, Canada Geese, *Branta canadensis*, apparently mate for life and the families remain together at least until the late fall (Elder and

Elder, 1949). Presumably there is some advantage to the reproductive success of the species in this behavior.

The relation of courtship performances to territory is perhaps the most difficult to analyze. It seems likely that the original territory was around the site for copulation and that the territory has been extended both spatially and temporally. The courtship behavior serves to keep the pair united until a territory can be staked out. Kingbirds, *Tyrannus tyrannus* (Davis, 1941) pair before establishing a territory and perform courtship displays actively until the territory is firmly outlined.

This summary of the relation of the nesting cycle to courtship indicates that, at least in many species, the courtship behavior can have the function of keeping the pair together until the requirements of reproduction are satisfied.

TERRITORY AND REPRODUCTION

Territorial behavior is well known in all its multiplicity of forms. In general, it consists of song, posturing, or actual fighting, all of which serve to stake out a claim for land. In some sea birds that nest on cliffs the land may be only a foot or so in diameter. In some hawks the land may be several square miles. Many passerine birds have a territory of about one or two acres. It is not the purpose of this discussion to describe the details of the social behavior that is involved in the defense of the territory because the chief objective is to try to understand how social behavior, as reflected in territorialism, affects reproduction of the species.

If we assume that the primordial function of territorial behavior is to provide a site for copulation, then it is clear that this form of social behavior fosters reproduction and indeed seems necessary for reproduction. The tiny territories maintained by Gould's Manakins are adequate to ensure that reproduction can occur because the males are not interrupted during coition. Many other species require little more than a copulatory spot. The Ruff, many grouse, and many hummingbirds have only a limited duration of time for the relation of social behavior to reproduction.

Other species have a restricted territory around the nest. Some are colonial nesters, such as gulls, herons, and jackdaws, while some are practically solitary as, for example, some birds of prey. Again we conclude that, since these species are thriving, their social behavior is adequate for the maintenance of reproduction.

Still other species regulate their reproduction by means of social behavior that obtains an area of ground around the mating and nesting

site. The Great Crested Grebe, *Colymbus cristatus* (Huxley, 1934) and the Goldfinch, *Spinus tristis* (Stokes, 1950) defend a territory around the nest site but obtain most of the food elsewhere. We deduce that in these species their life history is such that it is unnecessary to have a social behavior that will obtain a feeding ground to ensure reproduction.

Perhaps the majority of passerine birds have a territory that includes a feeding area. For success in reproduction it seems necessary that the social behavior provide the means for obtaining adequate food. This is the classical territory as described by Howard (1920) for the buntings and warblers. In some species (Song Sparrow; Nice, 1943) the young are fed within the territory even after they have left the nest, but in other species (Black-capped Chickadee, *Parus atricapillus*, Odum, 1941) the young leave the territory a few days after fledging and are fed outside the territory. Howard in his chapter, "The relation of territory to the system of reproduction," discusses the food problem in great detail. I wish to defer my discussion of this problem till later in order to develop the background further.

In a small number of species, a colonial territory is defended by the birds. Rooks, *Corvus frugilegus* (Yeates, 1934) defend a territory as a group but remain in pairs for nesting. The anis (Davis, 1942) show the evolution of a colonial territory. A primitive species, *Guira guira*, defends a colonial territory, but the colony frequently divides up into pairs which defend a small territory within the colonial territory. Another species, *Crotophaga major*, nests communally, but the birds remain paired. The most evolved species, *C. ani*, nests communistically and has lost all social behaviors associated with pairing. The abundance and wide distribution of this species is proof that reproduction is adequate and that the social behavior associated with pairing is quite unnecessary for these conditions.

THE HIERARCHY AND REPRODUCTION

Social behavior is related to reproduction in still a third manner. Many species that live in groups develop within the group a ranking that is called the social hierarchy. The individuals in the group arrange themselves in order according to their dominance which usually depends upon strength in combat. Guhl and Warren (1946) showed clearly that the dominant cock in a group of three cocks fertilized more eggs and sired more viable chicks than did the other two cocks. Presumably this relationship holds for other species that have a social hierarchy. This behavior is thus positively related to reproduction by ensuring that the dominant individual produces most young. In

times of scarcity of food or other necessities it seems likely that the dominant individual will obtain his requirements and the subordinate individuals will starve. But reproduction will continue at about the same rate since the dominant individual performs most of it anyway in polygnous species. Thus the social behavior that produces a hierarchy enables the species to maintain reproduction in times of hardship.

DISCUSSION

We have now surveyed the relations of social behavior to reproduction and seen that three types of activities are involved: (1) courtship, (2) territory, (3) hierarchy. In all three types there is great variation of behavior from species to species, but we have concluded that, because a species is thriving or at least not extinct, the social behavior is adequate for reproduction. But this type of reasoning is circular and resembles the "survival of the fittest" reasoning that annoys the philosophers and logicians. Just as we define the fit as the ones that survive so we define adequate social behavior as that of the successfully reproducing species. This logical problem has not yet been resolved to the satisfaction of all in the evolutionary controversy, and even today there exists little experimental evidence that the fit ones actually do survive better than the less fit. Hence, we should not be discouraged in our attempt to obtain proof for the thesis that these social behavior patterns are adequate and necessary for reproduction.

Another difficulty with the present state of the thesis is that we have little evidence concerning the possibility that a change in social behavior might improve the reproduction of the species. We can very well ask, "Would Song Sparrows reproduce better if they had a colonial feeding territory or some other modification of their social behavior?" The evolution of social behavior in the Crotophaginae suggests that such changes may be beneficial. The least successful of the species, *Guira*, pairs and frequently defends a nesting territory. It is nowhere abundant and has a limited distribution in southern Brazil, Uruguay, and Argentina. In contrast, the most successful species, *Crotophaga ani*, has lost all pairing behavior. It is abundant throughout a wide range from southern Argentina north to the United States and including the West Indies. But without experimental analysis of the factors governing the population it is impossible to conclude that a change in social behavior caused an increase in population. All we can say is that the two are correlated.

The difficulty of experimentally testing the theory of territory bothered Howard, and he actually performed some experiments to

determine whether it was necessary that the adults have a supply of food within a short distance. His experiments agreed with the theory but were inadequate to prove anything conclusively. But unfortunately Howard developed the food requirement idea and hence received criticism from many persons, especially David and Lambert Lack (1933). This criticism pointed out that many species do not defend territory when they need food most, that is, after the young are hatched. Furthermore, there is little evidence that territory limits the number of pairs in a region.

The procedure for determining the factor that limits reproduction (or a population) is exceedingly complex. But this problem is basic to an understanding of the relation of social behavior to reproduction and also to determining the functions of social behavior. Let us therefore digress for a while into a discussion of regulatory factors and limiting factors. A regulatory factor affects the success of reproduction in some manner. For example, viability of sperm determines how many eggs are fertilized and thus affects reproduction. Similarly, courtship behavior must be adequate to stimulate copulation, and hence it affects reproduction. Or high temperature may hinder development of the embryos and hence may affect reproduction. It is obvious that there are a multitude of regulatory factors that are inextricably interrelated. Furthermore, the intensity of the effect may vary from year to year and from place to place so that an almost hopeless jungle of relations develops. Fortunately, however, some factor may act at a particular time and place as the minimum factor to limit the reproduction. This, of course, is similar to the situation described by the phrase, "A chain is no stronger than its weakest link." The regulatory factor which at a definite time and place determines the extent of reproduction is called the limiting factor. Thus it is possible that viability of sperm would be so low under certain conditions that only a small proportion of eggs would hatch. Under these circumstances courtship performances and food supply would be more than adequate for the few young. Or at some time courtship might be impeded by unfavorable conditions so that the fertility or food supply would be far in excess of the number of young. Or in some place the food supply might be inadequate for the young and hence limit the number raised. These examples are far simpler than nature usually is, but they should demonstrate that the limiting factor acts upon a particular relationship at a particular time and place.

For an understanding of the relation of social behavior to reproduction it is necessary to digress once more into the problem of limiting factors. Of the many factors that regulate reproduction of a popula-

tion of birds, or the population itself, competition within the species is frequently the limiting factor. Birds have largely avoided the limiting effects of ordinary variations of environmental factors by the development of migration, of homoiothermism, of incubation, and many other adaptations. Similarly birds have largely avoided the limiting action of predators and disease by developing protective coloration or behavior, or immunity and tolerance to infection. Thus these two groups of factors rarely in nature become significant as the limiting factor. Such climatic catastrophies as the sleet storm that practically destroyed the Bluebird, *Sialia sialis*, population of New England in 1908 or such epidemics as occurred in duck populations (Rosen and Bischoff, 1949) are, fortunately, not daily occurrences. The result of this situation is that the limiting factor in reproduction is usually some form of competition which obviously involves social behavior.

Let us now return to a specific example of the relation of social behavior to reproduction. Consider the classical case of the relation of territory to food supply. For Yellow Buntings, *Emberiza citrinella*, Howard concluded that a territory was necessary to provide adequate food for reproduction. This implied that food supply for Yellow Buntings regularly was the limiting factor and that other regulatory factors such as temperature, disease, predators, and nesting sites were all ineffective in limiting the reproduction. Under these circumstances the number of young produced depended upon the social behavior of the adults that ensured an adequate food supply. To quote from Howard, "This end the territory serves to promote; it roughly ensures that the bird population of a given area is in proportion to the available means of subsistence, and it thus reduces the risk of prolonged exposure to which young are always liable."

But subsistence is not always the limiting factor, and Howard gives an excellent example of the exchange of factors that limit a population. Under usual weather conditions the territory contains enough food so that the adult Yellow Buntings can find food and return to the young in time to prevent their chilling. But June of the year 1916 was exceptionally cold and the adults could not get enough food fast enough. Hence a high mortality of young resulted. The limiting factor in that year was therefore cold weather rather than territorial behavior.

Another example is provided by the data for Song Sparrow populations (Nice, 1937). From 1930 to 1935 the number of males varied as follows: 33, 31, 44, 29, 19, and 17. In brief, the history was that in 1933 there was a considerable destruction of cover, but that espe-

cially in 1931 and 1932 the environmental conditions were essentially the same. However, in 1931 there was a scarcity of Song Sparrows (only 31) in contrast to a population of 44 in 1932. Therefore, in 1931 some unknown factor, perhaps a winter mortality, had limited the population. But in 1932 almost every available piece of land was utilized, and hence the social behavior of territorialism limited the population. It is quite obvious that whether or not social behavior limits reproduction depends upon the circumstances.

We thus find that social behavior may and frequently does have very complex relations with reproduction. These relations are both on an individual basis and a population basis. We also find that it is extremely difficult to explore the relationships because of the difficulty of detecting the limiting factor in a particular situation. It is appropriate therefore that we outline some of the methods of testing the hypothesis that social behavior, as manifested by courtship, territorialism, or hierarchy, affects the reproductive rate of a species.

Perhaps the first method should be experimental. To test the hypothesis it is necessary to make certain that all other regulatory factors are available in excess of the requirements of the species and that an excess population of birds is present. It must then be observed that by means of some social behavior the reproduction is affected. An example is found in Nice's Song Sparrows for the year 1932. Apparently there was an ample population of birds and more food and shelter than needed. But the data are not sufficiently detailed to show that birds actually were driven from the area by territorial fighting. We can always ask the question, "Could another pair have squeezed in, if it had been present?" In 1933 the amount of cover was reduced and apparently became the limiting factor. It is impossible to claim that territorial behavior limited the reproduction that year because, according to the map, many of the territories did not join another territory.

An experiment with Barn Swallows, *Hirundo rustica*, is in progress and may be described although the results show nothing yet. These swallows are only slightly territorial but do defend a small area around the nest. The large barn under observation has an unlimited supply of nesting sites under the rafters and an ample supply of nesting material. The food supply is presumed to be ample because the swallows have for their use extensive fields and a barnyard with many animals. The supply of birds also is presumed to be ample because the species is abundant in the region. There is unfortunately no proof that these assumptions are true each year. However, under these conditions the number of swallows nesting in the barn should be limited by the

territorial requirements of the birds, that is, the social behavior should affect reproduction. This limitation should be manifested in a fixed upper limit to the population, at which time excess birds would be driven away. In 1949, eight pairs nested in the barn and in 1950, 18 pairs nested there. Clearly in 1949 the social behavior was not the limiting factor since in 1950 many more pairs were accommodated. Only additional evidence will tell whether 18 pairs is the maximum number. It should be possible to alter the number of nesting sites and thereby test the relationships.

Another experimental observation may be revealing. On an island in the Chesapeake Bay, four pairs of Ospreys, *Pandion haliaetus*, have nested since 1946 and according to the farmer for many years before. The birds are regularly spaced in the available area, although there seems to be plenty of food and nesting sites. In 1950 a fifth pair unsuccessfully tried to nest on a duck blind near the island, although more usual nest sites were available. It seems likely that social behavior restricts the number of breeding pairs to four on this island.

Another method for examining the thesis is to observe carefully the social behavior and relate it to success or failure of individual birds. Davis (1941) noted several times that the Kingbirds built nests but abandoned them. In one case a nest was started in an oak but abandoned. The pair nested later in an apple tree. In another case a pair built three nests in succession but never laid eggs. Hochbaum (1944) cites a case of a male Canvasback, *Aythya valisineria*, that lacked a territory. When he tried to copulate with his mate, other drakes interfered, showing that territory is essential in this case to reproduction. Indeed, in many species copulation outside the territory may be interrupted by other members of the species. As another type of failure, Skutch (1931) found that the cause of half of the nesting failure of Rieffer's Hummingbird, *Amazilia tzacatl*, was pilfering of the nest by other hummers. We can also obtain data of this type on the population level. The Heath Hen, *Tympanuchus c. cupido* (Gross, 1928) may have become extinct because the number of birds was so low that adequate social behavior was not attained. But to prove this contention requires very detailed observations. The same explanation has been given for the extinction of the Passenger Pigeon, *Ectopistes migratorius*. If enough observations of this type can be related to presence or absence of social behavior (courtship, territorial, or hierarchal behavior), then perhaps a causal correlation can be detected. This will be difficult because of the complexity and infrequency of observations and an understandable reluctance to study birds that failed to nest.

A last method for studying the thesis is by a comparative study of a group of closely related species. The studies of the Crotophaginae (Davis, 1942) have already been mentioned. The evidence available for three species suggests that low reproduction was correlated with the social behavior of territorialism and that high reproduction accompanied the loss of territorialism. This is no more than a correlation and is particularly weak because nothing is known of the mortalities of the several species.

Another example of comparative behavior is Friedmann's study (1929) of cowbirds. The two species that have lost their territorial behavior, *Molothrus ater* and *M. bonariensis*, are eminently successful as judged by their abundance and wide distribution. The territorial species are less successful, but again we know too little about the other factors to conclude much about relation of social behavior to reproduction.

Moreau and Moreau (1938) compared two closely related weaver finches. In one species, *Euplectes hordacea*, the maintenance of territory seems to limit the population, while in another species, *E. nigroventris*, the territories seem to be indefinitely compressible and hence do not limit the population. Unfortunately data directly applicable to the hypothesis are usually suitable for the development of correlations but not causal relations. Much work remains to be done in this complex field before the extent of causal relations of social behavior to reproduction can be determined. Let us illustrate the problem in its simplest terms. Given a species that performs social behaviors, A, B, and C, and reproduces at a known rate, what will that rate be if behavior C or B or A is eliminated? Or if behavior D is added or substituted? We now can rarely prove that these complex social behaviors have any significant effect on reproduction. They may merely be useless or at least innocuous accompaniments to the reproductive cycle. Until we can find out what happens in the absence of these behavior patterns, we will have to be content with tentative deductions based upon correlations.

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SOCIAL BEHAVIOR AND SURVIVAL

BY F. FRASER DARLING

THE convener of this symposium has given me the enviable position of being the last speaker on the program (see Auk, 69: 127–182, 1952), but he has offset that by giving me the most difficult subject—at least so it seems to me—of social behavior and survival. One can certainly talk about gregariousness, the *development* of social behavior, and the fundamental factor of sociality in reproduction, but to be faced with commenting on social behavior and survival I feel that I am in serious danger of being teleological or of picking facts to support an argument, and that will never do. Perhaps it would be easier to show the part of social behavior in survival of the individual or of the species by a study of negative evidence, but we should all have a tedious half-hour.

Social behavior and survival are so closely linked that I feel I can do no more than emphasize the obvious. The animal cannot truly stand alone and, as we are now coming to understand, neither can a good many plants. The whole trend of ecological thought at present is towards a realization of the importance of community, and in this respect we are becoming increasingly aware of the social interactions between species and the whole complex of the ecologic association. But, of course, I must not beg the question by calling on the wide ecological field. The animal, as I say, cannot truly stand alone; the social interest is there, implicit and inherent, mainly to be derived—as I believe—from the fundamental need for reproduction. But there is more to it than that. I believe an animal needs to go outside itself, just as we do, and to enter into relationships with others of its kind. There seems to be in animal life a reciprocal responsiveness which in itself leads to a development of variability of behavior—and there can be no evolution without variability. It would be unscientific to say that this generic need for the awareness of other selves is designed to lead towards cooperative behavior, but cooperation undoubtedly develops. That inherent, unconscious, reciprocal responsiveness is, in fact, cooperation in its simplest sense.

How does this view square with the orthodox biology of the later nineteenth century? Darwin based his theory of natural selection on the survival of the fittest. There was an interminable struggle for existence. Darwin's followers took the bald hypothesis farther than he would have been prepared to go, I think, and the notion of "Nature red in tooth and claw" blinded us to the complementary notion of evolution, which implied survival, continuing through cooperative

effort as well. Kropotkin (1902) was so ingenuous and lacking in critical outlook that he may have retarded the emergence of a scientific view of sociality and survival.

It is only recently that zoological workers and those in comparative psychology have realized that the group is a major ecological factor in the life of the individual. Sociality is fundamental in life and not a cultivated development of the so-called highest form. Allee, in Chicago, has done 30 years of investigation of animal communities in the comparatively low forms of life in which we are not accustomed to acknowledge a high type of possibly conative behavior such as we see in some birds and mammals. It is his view that many advances in evolution may have come about through selection of cooperating groups rather than of individuals, and he has stated the beautiful concept that the two great natural principles: struggle for existence and cooperation, or reciprocal responsiveness, as I prefer to call it, are not wholly in opposition, but that each may have acted on the other in determining the trend of animal evolution. My own work has been confined to birds and mammals. In the study of a herd of red deer I found that sociality was intrinsic and, at least to my own satisfaction, it was clear that social behavior was intimately bound up with survival. The study of *behavior* in birds is fairly recent among men of science. It received its greatest impulse from the publication of Eliot Howard's (1920) researches on territory, work which in some ornithologists' minds tended to emphasize those types of territorial behavior which lead to the segregation of pairs, to active hostility to neighbors, and to independent or isolated behavior. Consequently, the social behavior of birds was somewhat overshadowed until a few years ago, since when numerous researches have not only enlightened us on this subject alone, but have given us new concepts in the study of evolution.

My own research on avian sociality was published over 12 years ago. It held the dual thesis of—the reality of social stimulation to reproductive condition in such birds as are social or colonial at some state of, or throughout, the breeding cycle; and the existence of a threshold of numbers in some colonial species, which might be critical as to whether the birds bred or not.

Naturally, the extent to which the social factor enters into the life of birds varies greatly. In some it appears to be sporadic, in others seasonal, and in others it constitutes the whole way of life. Whereas the benefits of sociality in the lower animals as studied by Allee (1931, 1938) and others appear to be physiological in origin, operation, and result, the basic element of *stimulation* in avian sociality seems to be psychological and psycho-physiological.

The life of a bird falls mainly into two linked parts—maintenance of its everyday activities and reproduction of its kind. Let us take some examples of aggregations and sociality in the maintenance activities of birds. It is obvious that within a population where members share a common medium as food, with common methods of obtaining it, flocking or grouping at a feeding ground is likely to arise, and it is one of the simplest forms of gregarious activity—an assemblage without any special social cohesion at a place of abundance of food. We do not know for sure whether these aggregations have survival value, though in some fishes and among domestic hens Allee found that more per head is eaten when several are present than when the creatures are solitary. The farmer observed the phenomenon in little pigs long before, but you may question the survival value of eating more, for it has been shown in the laboratory rat that a measure of inadequacy in food increases the life span. Gallet (1949) tells us that the Flamingo, *Phoenicopterus ruber roseus*, never feeds alone, unless it is ill or injured. As a species it is one of the most tightly coalesced into flocks. Bartholomew (1942), observing Double-crested Cormorants, *Phalacrocorax auritus*, in San Francisco Bay, showed that a flock of these birds was more active in fishing than individuals fishing alone, and the activity of a larger flock was greater than that of a smaller flock. Different methods of fishing were evident between large flocks, small flocks, and birds fishing alone. Bartholomew concluded that mass fishing was efficient, as a surprising number of birds made catches. The formation of one of these large fishing flocks is interesting. The first group to alight does not begin feeding but swims about slowly till other flocks join it, and it is thought the birds locate a large flock by sight. Bartholomew suggests that birds of a large flock are stimulated to maximum effort by the presence of a large number of easily-caught fish, but if this is so, they are not so stimulated by the fish alone, or the first-comers to the scene would become active immediately. A flock of Starlings, *Sturnus vulgaris*, searching pastures for insects move rapidly over the ground, each bird spurred on by its neighbors, and if one should startle an insect from a tuft of grass, a neighbor may obtain it, whereas the insect would perhaps have escaped if it had been startled by a solitary bird.

Simple assemblages of birds are typified by winter roosts of Starlings, finches, wagtails, and Wood Pigeons. Once more we cannot assess the survival value of such aggregations, but for the Starling the physical possibility of conservation of heat should not be overlooked. The rise of emotion in the roost resulting from numbers may in itself bring about physiological conditions helping the bird to endure the environ-

mental stress of the long winter night. But, of course, we do not know, and it would be valuable if the physiologically-minded from among us would devise some experiment for finding out. The onset of cold is a potent factor causing flocking in small birds.

The complicated and intricate structure of the multispecific flock has not yet been thoroughly studied, but Colquhoun and Morley (1943), working with tits, have found that the aggregation is evidently not merely for the sake of feeding, because each species tends to have its own vertical niche in the flock and is therefore feeding at a different level from the others. If the species are feeding in roughly stratified fashion, why need they feed together? Whatever the purpose, it must be fairly important, for with the Marsh Tit, *Parus palustris*, one of the species found in the flock, over 70 per cent of some ringed individuals were found in a flock for the eight months June to January. The concerted cries and call notes of the flock actually render it conspicuous to predators, more loudly declare its whereabouts, than if individuals were scattered.

Similarly, Roberts (1942) in Australia has described the winter flocking of the Pied Currawong, *Strepera graculina*, in which species it would seem that social contact stimulates psychic and physical qualities and that the common activities of the flock have a real, though not obvious, value in maintaining biological fitness during the non-breeding season.

Leaving aside the apparently haphazard aggregations, which still must not be dismissed as being without order, there are the flocks in which organization is obvious.

When we examine the social factor in relation to reproduction, we have more evidence than we have for maintenance. As one who has been responsible for postulating that social stimulation is of value in synchronization of breeding condition and that the display of the social group has value for the individuals, I do want to say that it is obvious that such a state of affairs does not appear in many species, and the principle does not apply all round, but that fact does not invalidate the principle in those species which *are* social and colonial nesters. Even here the principle varies in intensity and may be modified by fluctuating ecological conditions. It is not a good enough argument to say that because on two occasions a single pair of Gannets, *Morus bassanus*, has occupied a rock and nested successfully that the principle of social stimulation to breeding success does not apply in this species. The Fulmar Petrel, *Fulmarus glacialis*, appears to be a species in which the social factor is critical in reproduction. My own evidences, published in 1938, were slight, but they have since been con-

firmed statistically by Fisher (in press) who has just completed a monumental study of this species. There can be no doubt of the greater biological success of the larger colonies and the figure of 8 to 12 pairs seems correct for the all-or-none reproductive threshold. As an example of how social nesting may *adversely* affect survival, I should mention the work of Lees (1946) on the Rock Dove, *Columba livia*, who shows that where the species is colonial, if one pair deserts or loses its nest, the other pairs in the colony follow suit.

There is not space to go through the body of work published in the last ten years which supports the biological survival value of social stimulation. Instead, I want to draw special attention to what we call aggressive behavior and its place in social stimulation. True fights do occur, but they are rare, and I think that the uniqueness of the combative nature of our own species tends to make us interpret the formalized fighting of birds too literally. Aggressive display is one of those facets of the complex of bird life which evolution has seized upon for development of a different kind. For example, in Johnson's study (1941) of the Atlantic Murre, *Uria aalge*, a bird in which crowding seems a necessity for reproduction, he observed frequent fights regardless of sex. The fights seemed to intensify the urge to incubation rather than vanquish a neighbor as a competitor for space. The greater the amount of fighting, social preening, crowding, and calling, the greater the amount of apparent general satisfaction and welfare. Crowding occurs in spite of there being unoccupied ledges. Lockley (*in litt.*) found much the same conditions on Skokholm, and so did I on North Rona. Perry (1940) found that the tempo of activity of individuals of this species without young increases when hatching of the eggs of a colony causes an increase in the fishing activity of the parents and that on crowded stacks the delivery of the fish to the chick tended to be more immediate than on sparsely populated ledges. This, of course, could be interpreted that the avarice of neighbors, and fear of having the fish snatched from them, caused parents on crowded ledges not to dally in passing the morsel over, but Perry elsewhere observes that if the parent does so dally the chick often abandons its attempts to secure the food and burrows again into its brooding parent.

Williamson (1949) remarks on the aggressive flight of the Arctic Skua, *Stercorarius parasiticus*, against human intruders being common throughout the nesting cycle in the colony, but absent from the behavior of solitary pairs. He suggests that this behavior needs a certain level of mutual stimulation not attainable by solitary or widely scattered pairs. Williamson also mentions that Arctic Terns, *Sterna*

paradisaea, strike the intruder more readily in large than in small colonies.

It is perhaps significant that species living in a difficult and hazardous environment are social in the breeding season, a sociability reaching extreme lengths in the Emperor Penguin, *Aptenodytes forsteri*, where incubation of the egg is shared among a group. Other birds, such as the Flamingo, Sandwich Tern (*Sterna sandvicensis*), and Shelduck (*Tadorna tadorna*), form crêches, the young banding together and being reared by adults not necessarily their parents. There is a strict adherence to age-groups in these crêches. This is definitely of value for survival, for fledglings of contemporary age and powers band together into a more compact flock than one composed of youngsters of different levels of performance; and the more compact the band the safer are the individuals composing it from their predators, the gulls.

Many species of birds which nest in separate, fairly extensive breeding territories, and which establish and defend these by apparent fighting are for the most part indulging in no more than aggressive display. May (1949) remarks that a group of territories of the Willow-Warbler, *Phylloscopus trochilus*, by reason of the volume of song, has more chance of attracting females than has an isolated territory. Even with the pugnacious European Robin, *Erithacus rubecula*, Lack (1948) finds that winter territories in English woods tend to be bunched, though the conditions overall seemed so similar that they could have been widely separated. He says, "Perhaps the singing of one individual, though repelling others from the actual territory, attracts them to settle near by." Nice (1937) observed the bunching of territories of the Song Sparrow, *Melospiza melodia*, apparently from preference and not from limitation of the habitat. Bickering was frequent on the peripheries. Likewise Yeates observed a tendency for the territories of Snow Buntings, *Plectrophenax nivalis*, to be together. Armstrong (1947) says the birds, in spite of their territorialism, are attracted to each other and benefit, by mutual stimulation. My own remark here is that the phrase "in spite of territorialism" is as a pair of blinkers to the point of view that territorialism is one aspect of social behavior. The aggressive quality of bird song has, I think, been overemphasized. Proclamation, yes; *apparently* aggressive, yes; no more combative than a military tournament of befrogged dragoons, but probably even more stimulating. So-called fighting, and singing, are in my opinion often a form of social stimulation and have indirect survival value as aids to development of reproductive condition. I should think the term "aggressive behavior" could be dropped for a great deal of true display.

Morley (1941) found in Starlings that the eviction of interlopers to the territory caused the members of a pair to display to one another, and that owners' visits to nest sites in their territory greatly interested their neighbors. She also found in Marsh-Tits (1943) that after territorial clashes the pair was stimulated to visit possible nest sites. Ruttledge (1946) notes in the Irish Coal-Tit, *Parus ater hibernicus*, that the volume of song is much dependent on birds of adjacent territories being close to one another. A bird whose territory is seldom invaded or which spends much time in the center of the territory is rarely heard to sing. Perry (1940) records for the Puffin, *Fratercula arctica*, that the mere sight of another Puffin alighting on the same terrace provokes display between the pair, and so do squabbles between neighbors, while *display* or vocalizing in burrows stimulates a great deal of interest among other Puffins around.

The most highly developed social aggressive display is apparent in some game birds such as the Blackcock (*Lyrurus tetrix*) and the Prairie Chicken (*Tympanuchus*), and in some waders such as the Ruff (*Philomachus pugnax*). Here the formalized fighting has reached such a degree of organization that it is doubtful whether successful reproduction would be possible without it. The social stimulation is of critical survival value, but do not let us ever think of it as aggressive behavior.

I have been strengthened in this view in later observations in breeding territories in red deer and in Atlantic seals. Fighting does occur, but formalized fencing by stags and display of canine teeth and claws by bull seals is much more common. I have noticed in red deer that the large female groups mean several harems close together, which phenomenon means more challenging behavior on the part of the stags, and as the females in season solicit the stags in a beautiful courtship display, the stags are quicker in response when they are kept in a state of excitement by their challenging of other stags. The whole subject of challenge and vocal display needs fuller investigation as a social phenomenon with survival value.

The breeding behavior of the Lapwing, *Vanellus vanellus*, provides an example of a link between the social aggressive display of males and the social display between sexes and social nesting. Rinkel (1940) in Holland speaks of *colonies* of Lapwings, as a number of territories are always found together. He found that, far from avoiding clashes, the males seemed to need them and the emotional stimulation they gave, and the birds sought opportunities for them. Meanwhile the females do not desert the display ground for egg-laying, but lay in territories within sight and sound of their fellows.

I would like to put forward the hypothesis that one of the important functions of territory in breeding birds is the provision of *periphery*—periphery being defined as that kind of edge where there is another bird of the same species occupying a territory. One pair of warblers in a wood have, in effect, no territory at all; they are merely existing in space. But by pushing up against each other, rather than spreading themselves out, the birds are giving themselves peripheries, and there are doubtless optimum peripheries for each species. The breeding territory has little to do with a sufficiency of feeding ground for raising the brood. It is a place with a focal point or two—the nest site and the singing post—and periphery. Southern and Morley (1950) show that there is a considerable concentration of Marsh-Tits on what they call the "defended" boundaries of territories, with less interest in the neutral margins. If this hypothesis is correct, then *territorial behavior as a whole is a social phenomenon, and it has survival value.* We also begin to see functional survival value in autumnal territorial sexual behavior among birds (Morley, 1943).

We cannot go into the complicated subject of social flocking for migration and the possible survival value. Those who may have watched geese preparing for migration, and the behavior when they arrive at their wintering ground, the flocks having tended to break up and time being given to building up again before even feeding, can have little doubt that the social behavior has survival value for the individual and the species; but we do not have it well analyzed. Lorenz, in his "Kumpan" paper (1935), gave us new standards of inquiry, but we have not followed them up as fast as we might have. The field is varied and all of it is important, not only in bird studies but in comparative psychology and a whole socio-ecology which includes our own species. This symposium shows something of achievements and of deficiencies, and the best it can do for us here is to stimulate *us* to further research—social or otherwise.

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THE ALLEGHENY MOUNTAINS AS A BARRIER TO BIRD MOVEMENT

BY MAURICE BROOKS

THE Allegheny Mountains arise in New York and extend in a southwesterly direction to Virginia. A portion of the Appalachian system, they include a number of more or less parallel ridges, and, as the Allegheny Plateau of physiographers, comprise one of the major physiographic provinces of eastern North America. Beginning with elevations of 3,000 feet or less northward in New York and Pennsylvania, they rise to points almost 5,000 feet high in West Virginia and Virginia.

During Pleistocene times the Allegheny Plateau was, in its entirety, unglaciated. Northern portions were for long periods bounded on north, east, and west by extensive ice sheets. This exposed area extending northward into seas of ice must have exerted a profound influence on bird migration and nesting. It probably had a considerable effect on speciation and racial separation, if we could only read and interpret the riddles which the region holds.

Throughout most of its length, the main axis of the range, known as the Allegheny Backbone, is a secondary continental divide, separating waters which flow to the eastern seaboard from those which reach the Gulf of Mexico through the Mississippi system. The Allegheny Backbone is also a natural dividing line between Atlantic and Mississippi flyways for birds.

Because of elevation and abundant rainfall the higher reaches of the Alleghenies were originally clothed in dense coniferous forest, chiefly of red spruce and hemlock, but with considerable areas of white and pitch pine and other species. These mountains, therefore, constituted both a physiographic and an ecological barrier to bird movement. Probably the ecological influence was greater than was the physiographic. It may be supposed that bird species of the deciduous forest found spruce and hemlock woodlands uncongenial for both breeding and migration. Many species which fan out northward from the Gulf of Mexico seem to find a crossing of the Alleghenies difficult, even under present conditions. The converse is also true, since a number of Atlantic seaboard races and species do not regularly cross the Alleghenies.

Within the last hundred years most of the original forest over the Alleghenies has been cut, and much of the land has been cleared. Under these radically changed conditions the ecological barrier has

tended to become less effective, and many species and races are seemingly in the process of modifying their migration routes and their breeding ranges. Nevertheless, as will appear below, the Allegheny Mountains still exert a profound influence on bird movement.

RACIAL SEPARATION IN BREEDING

Among breeding birds of the region, there are a number of instances in which the Allegheny barrier seems to have influenced racial separation. A good example of this is to be found in the Eastern Yellow-throated and Sycamore Yellow-throated warblers, *Dendroica dominica dominica* and *D. d. albilora*. The Eastern Yellow-throated Warbler is essentially a bird of the southern Atlantic coastal pine forests. It reaches its northern limits in the region to the east of the Alleghenies, and it does not, to any great extent at least, invade the mountains. The Sycamore Yellow-throated Warbler reaches its northeastern breeding limits in the Allegheny Plateau along the Ohio River. Due to its white, rather than yellow, lores, it is morphologically quite distinct from the eastern race. More striking still is its difference in choice of nest sites. The Sycamore race, as the name would suggest, builds its nests in sycamore trees growing on the flood plains of sluggish streams. It is occasionally found on slopes away from streams, but even here its nests are often placed in deciduous, rather than in coniferous, trees. Southward of the Alleghenies there is a zone of overlapping of these two races, and individuals which are intermediate in morphological characteristics may be found. In the zone of overlap, nests may be placed in either deciduous or coniferous trees, but in the Allegheny region the two races are separated and distinct both as to physical characters and breeding habits.

Another example of racial separation at the Allegheny barrier is to be found in the Yellow-throats, *Geothlypis trichas*. According to Dr. Wetmore's determinations, birds of the Allegheny region west of the Backbone are of the northern race, *brachidactyla*, while the breeding Yellow-throats east of the ridge are of the Maryland race, *trichas*.

A striking example is to be found in the Grackles, *Quiscalus quiscula*. East of the Alleghenies the resident Grackle is the Purple Grackle, *Q. q. quiscula*, while to the westward only the Bronzed, *Q. q. versicolor*, is to be found. This is not the place to open a discussion of whether these birds are racially or specifically distinct, but the two populations are constant in their observance of this mountain barrier. Of course, there are the so-called "Ridgway" hybrids, but local collecting of breeding birds does not show many of these.

Perhaps not quite so pertinent is the case of the Carolina and Louisiana paroquets, *Conuropsis carolinensis carolinensis* and *C. c.*

ludovicianus. The Carolina race was seemingly restricted to coastal cypress swamps, and just reached the region east of the Alleghenies. The Louisiana race, however, nested in deciduous woodlands along larger rivers and reached the Allegheny Plateau region, as is attested by the observations of both Audubon and Wilson. In the breeding of these two races we have an ecological situation which parallels strikingly that of Eastern Yellow-throated and Sycamore Yellow-throated warblers.

RACIAL SEPARATION IN MIGRATION

In their patterns of migration certain species and races show a remarkable sensitivity to the Allegheny barrier. The example of Northern Gray-cheeked and Bicknell's Gray-cheeked thrushes, *Hylocichla minima minima* and *H. m. bicknelli*, is an interesting one. Northern Gray-cheeked Thrushes regularly migrate along both sides of the Allegheny Backbone, although they are usually considerably more abundant to the west than to the east. Bicknell's Gray-cheeked Thrush, however, is sharply restricted in migration to the region east of the Alleghenies. From the plateau west of the Backbone we have but a single definite record for this race, an individual taken by Lunk (Auk, 58: 264, 1941) near Morgantown, West Virginia.

The situation between Western Palm and Yellow Palm warblers, *Dendroica palmarum palmarum* and *D. p. hypochrysea*, is even more striking. In spring migration, Western Palm Warblers are unusual east of the Backbone. In autumn they occur eastward, although they are much more abundant westward. The Yellow Palm Warbler, on the other hand, is a common to abundant migrant in both spring and fall right up to the east slopes of the Alleghenies. It is so rare at any time in the region west of the Backbone that we have only uncertain sight records of its occurrence.

The situation of the Northern Water-Thrush, *Seiurus noveboracensis noveboracensis*, and Grinnell's Water-Thrush, *S. n. notabilis*, is somewhat similar. Northern Water-Thrushes breed as far south as the West Virginia mountains, and migrate on both sides of the Alleghenies, although they are much more common to the east. Grinnell's Water-Thrush is not known to breed in the Allegheny Plateau, although it does nest at Pymatuning Lake, Pennsylvania and Ohio, just outside the region. It migrates through the territory west of the Backbone, as has been shown by the collecting of Haller and others.

WARBLERS RARE EAST OF THE ALLEGHENIES

There are many wood warblers which migrate principally through Mexico, and which reach our borders in the Gulf of Mexico region.

Among eastern species are the Tennessee (*Vermivora peregrina*), Nashville (*Vermivora ruficapilla*), Cerulean (*Dendroica cerulea*), Bay-breasted (*Dendroica castanea*), Kentucky (*Oporornis formosus*), Mourning (*Oporornis philadelphia*), and Hooded (*Wilsonia citrina*). As might be expected, these species are common in migration west of the Backbone but are scarce east of it. Five of these species, the Nashville, Cerulean, Kentucky, Mourning, and Hooded warblers, remain to breed in the Allegheny Plateau. In the Allegheny region, all five are uncommon as nesting birds east of the Backbone.

It should be pointed out here, however, that changing conditions accompanying the removal of the forest are apparently affecting migration and breeding patterns of these species. Each year we have more reports of these birds eastward. Apparently the ecological barrier of the mountains is losing some of its force. To the northward in the Alleghenies, where the ridges are not so high, certain species have regularly crossed the mountains eastward to reach New England and the Maritime Provinces.

There is a curious situation as regards certain of the wood warblers which nest in the coniferous forests north of the Allegheny region. I mention it here, although I cannot explain it. One might suppose that such boreal species as Bay-breasted, Black-poll (*Dendroica striata*), Cape May (*Dendroica tigrina*), and Tennessee warblers would be common in migration in the Alleghenian spruce forests. So far as local observers can tell this is not true. Even in fall migration when these species are swarming in the lowlands, they are strangely absent from the heights.

INVASIONS

During the last 50 or 60 years the Allegheny region has been invaded by bird species moving in from south and west. These invaders include the Prairie Horned Lark (*Eremophila alpestris praticola*), Dickcissel (*Spiza americana*) and Eastern Lark Sparrow (*Chondestes grammacus grammacus*) from the west and the Black Vulture (*Coragyps atratus*) and Bachman's Pine Woods Sparrow (*Aimophila aestivalis bachmani*) from the south.

Forbush (Birds of Mass. and Other N. E. States, 2: 366 ff., 1927) gives an extensive review of the literature dealing with the eastward spread of the Prairie Horned Lark. Its appearances followed closely the removal of forests from the Great Lakes states and the Ohio Valley. It seemed to find little to impede its progress along the Great Lakes and in the lower northern portions of the Alleghenies. In the higher Alleghenies of western Maryland, West Virginia, and Virginia, how-

ever, the mountain slopes kept their original forests until a much later date, and while these existed they seemingly formed an effective barrier to the eastward spread of this bird. Only within the last 25 years have Prairie Horned Larks become common in the area just east of the south-central Alleghenies.

In the case of the Dickcissel we have, of course, an ornithological mystery. Just why it bred regularly on the Atlantic seaboard until about 1880 and then ceased to do so, no one can tell. Prior to that date there were very few resident ornithologists in the Allegheny region, and we do not know what the earlier status of this bird may have been in this area. In the late years of the nineteenth, and the early years of the twentieth centuries, however, it was certainly rare or absent from the region. About 1920, alfalfa began to be planted extensively in eastern Ohio, northern West Virginia, and south-central Pennsylvania. As an accompaniment to this new crop, Dickcissels began to appear in small numbers. They are now found locally, but regularly, in the Allegheny Plateau section of Ohio, and in western West Virginia. Still more recently, they have begun to appear sparingly in southeastern Pennsylvania, eastern West Virginia, and the region about the District of Columbia. In the territory east of the high, and generally heavily forested, Allegheny ridges, however, these birds are still practically unknown. In this case, apparently, the barrier is still effective.

The Eastern Lark Sparrow presents the case of an invading species from the west which occupied, and became common in, much of the westward Allegheny Plateau, reached the summits of the Backbone, and apparently receded from much of its newly-occupied range without ever crossing the mountains in numbers. Bird students of the unglaciated parts of Ohio are in agreement that the Lark Sparrow increased greatly in numbers and extended its range during the years around 1900. At about the same time, the birds began to appear regularly in West Virginia and western Pennsylvania. In 1901, Eifrig (Auk, 19:83–84, 1902) found them in numbers on the Allegheny Tableland in Garrett County, Maryland. By 1910 they were common breeding birds in central West Virginia, and they continued to be numerous there until about 1925. From that time to the present they have been generally rare and local throughout the region. During the entire period we have few, if any, definite records of the birds in the territory just east of the Alleghenies. It was not until 1932 that a Lark Sparrow's nest was found in Pennsylvania east of the Alleghenies. Boggs (Redstart, 3:91, 1936) gives the only two records for the species in West Virginia east of the Alleghenies—in Hampshire and Mineral

counties in 1936. No nest was found in western Virginia until 1937. In the case of this species, the Allegheny Backbone has certainly been an effective barrier to eastward movement.

Although its direction of invasion was different, the case of Bachman's Pine Woods Sparrow in the Allegheny Region closely parallels that of the Lark Sparrow. Long known from Kentucky, these birds seemingly crossed the Ohio River into unglaciated Ohio about 1898 and into West Virginia about 1900. During the early years of the century they spread northward and eastward through West Virginia and southwestern Pennsylvania until they reached the first high Allegheny ridges. Here their invasion was checked, and the birds gradually decreased in numbers throughout the Allegheny Plateau region without ever making a successful crossing of the Allegheny Backbone.

In more recent years Bachman's Pine Woods Sparrows have seemingly made another invasion and extended their range northward through the Shenandoah Valley to the east of the Alleghenies. They are now locally common in portions of northwestern Virginia and the Eastern Panhandle of West Virginia. We still have no evidence, however, that they have crossed the Backbone.

Black Vultures have in recent years certainly become much more common in the territory just east of the high Allegheny ridges. They are, today, fairly common in sections of western Virginia, eastern West Virginia, and central Maryland. One would suppose that for such strong fliers the Allegheny ridges would present no barrier at all, but the fact remains that in only one area have they established themselves in any numbers west of the Allegheny Backbone. From most of the Plateau there are no records whatsoever.

The case of the single establishment west of the Alleghenies is an interesting one, demonstrating the use of a natural port of entry. The New River, rising in North Carolina and flowing northwestward across Virginia, cuts through the high southern Allegheny ridges at Narrows, Virginia, and enters West Virginia shortly thereafter. Northward from Narrows there is a long, and virtually uninterrupted, valley extending through Monroe, Greenbrier, and Pocahontas counties, West Virginia. This valley lies directly west of Allegheny Backbone, and throughout its length Black Vultures are present in fair numbers. Outside this valley there is not a single record for the species in that part of West Virginia west of the Backbone.

CROSSOVERS

Despite what has been written above, it is obvious that many bird species in their migrations must regularly cross the Alleghenies.

Nearly 50 years ago Eifrig was wise enough to speculate that almost any waterfowl species found on Chesapeake Bay might also be found in the mountains of western Maryland. With the construction of artificial lakes in the Alleghenies of Maryland and West Virginia, his speculations have proved to be correct. We now know that a major waterfowl flyway from Lake Erie to Chesapeake Bay crosses southwestern Pennsylvania, western Maryland, and northeastern West Virginia.

There are certain species, both of land and water birds, whose crossing of the Alleghenies in our area is particularly interesting. One of these is Bonaparte's Gull, *Larus philadelphia*. Both in spring and fall these birds may often be found flying over woodlands and mountain meadows, often many miles from an extensive body of water. Their course is generally northwest-southeast, apparently in passage between the Atlantic Coast and Lake Erie.

Two species of migratory passerine birds, the Western Palm Warbler and the White-crowned Sparrow, *Zonotrichia leucophrys*, are often so abundant on the Allegheny crests in autumnal migration as to suggest a major traverse of the mountains. We know, of course, that Western Palm Warblers appear on the Atlantic Coast farther south, so this crossing seems logical. As to the movements of White-crowned Sparrows, we do not yet have sufficient information to justify a guess as to their destination.

The Allegheny Mountains have been here for a long time. They were uplifted in Palaeozoic times, and they have been continually above ice and water. When we know more of the movement of birds along and across them, we can, perhaps, begin to unravel some of the mysteries of migration and speciation.

Division of Forestry, West Virginia University, Morgantown, West Virginia, August 9, 1951.

GENERAL NOTES

Discovery of an Unrecorded, Mounted, Male Specimen of the Labrador Duck, *Camptorhynchus labradorius*.—About 1947–1948 it was reported that another specimen of the Labrador Duck had been discovered in England. Mr. R. L. E. Ford of Messrs. Watkins and Doncaster, London, who discovered and purchased the bird, informs me that it was mounted and a perfect drake. The specimen was found in a case of various mounted birds of North America in a country house where it had been about 100 years, but nothing was known of its history. The wooden base supporting the bird was screwed to the floor of the case by a pre-nettle-fold screw, *i. e.* not tapered. Mr. Ford sold the bird to a private collector in Britain, but he is not at liberty to disclose his name or the price, which was substantial. Information has reached me from other sources that the specimen was found in Kent and was sold to Capt. Vivian Hewitt for 500 pounds, after having been offered to the British Museum. Phillips ('A Natural History of the Ducks,' 4: 57–63, 1926) gave a list of 50 specimens which were then in existence; if no more have been added since that date, the total now reaches 51. The Labrador Duck did not become extinct until at least 1878, in which year one was obtained on December 12, near Elmira, New York (Amer. Nat., 13: 128, 1879). I thank Mr. R. L. E. Ford and Sir Norman B. Kinnear for assistance.—WILLIAM E. GLEGG, *Zoological Museum, Tring, England.*

A Peculiar Pigmentation.—The throat feathers of adult males of a South American Cotinga or Fruit Crow, *Querula purpurata*, have a peculiar pigmentation which was called to my attention about 48 years ago by the late Dr. C. W. Richmond. I made as much of a study of the phenomenon as was possible at that time, but I have delayed publication, hoping that a microchemical method might be devised for analysis of the pigments involved. No such technic, however, has as yet come to my attention, and I do not feel warranted in waiting longer for it.

When a lighted match or cigarette is held close to, but not touching the feathers mentioned above, their color changes quickly from a dark crimson red to a light orange. This change takes place in the distal exposed portion of the feather, *i. e.* the part not covered by other overlapping feathers, and here the feather structure consists of highly-modified, barbuleless barbs.

These barbs are flattened and twisted so as to present a maximum surface area for color reflection. Cross-sections reveal features which are unique in my experience.

The feather barbs of many species of birds have been studied by myself and by others. In all descriptions that have come to my attention and in all other cases which I have examined, the feather barb has a cortex surrounding a medulla and both may be highly modified. The medulla, however, always has relatively large air- or gas-filled cells. This arrangement does not occur in the structures described in this article. There is an outer layer that is almost too thin to be called a cortex. It is only two to four microns thick, and it has a pale, yellow color when viewed by transmitted light. Black pigment occurs more or less discontinuously at the outer surface and in granules occurring sparsely and irregularly in the interior of this layer (Fig. 1).

This cortex or cuticle covers a homogeneous, pigmented, central core which has a maximum thickness of about 20 microns, and in which no trace of medullary cells could be found. This pigmented central core when viewed by transmitted light in paraffin sections, ten microns thick, is orange-red in color. Similar sections of barbs,

IGURE 1. Cross-section of a barb of a throat feather of *Querula purpurata*. 800 ×.

after the application of heat, have an orange-yellow to yellow color in the core. The pigment has not faded in sections which were mounted in xylol-balsam, several years ago. A cross-section of a barb showing this phenomenon is shown in Figure 1.—R. M. STRONG, *Chicago Natural History Museum, Chicago 5, Illinois.*

Vestigial Claws on the Wings of the Kiskadee Flycatcher, *Pitangus sulphuratus caucensis*.[1]—In a collection of Colombian birds made by Father Antonio Olivares are 13 specimens of the Kiskadee Flycatcher, all taken within a radius of 15 miles of Cali, Colombia. Of these 13, three were taken at one place, Arroyo Hondo, and may well have been members of a closely knit group, perhaps even of one family, although one of them was collected a month before the other two, the latter birds being collected together. Each of these three (each an adult male) has a noticeable, exposed digital claw on each wing; the other 10 specimens, taken in the general vicinity of Cali and at Jamundi, some 15 miles away, show no sign of any such claws. A very extensive series of most of the races of this flycatcher has been examined and no additional cases of vestigial wing claws were noted. In his survey of the occurrence of such structures, Fisher (Amer. Midl. Nat., 23 (1): 234–243, 1940) found no wing claws on any passerine bird, although he examined some 241 specimens of 68 genera of some 20 families of the order. In other groups of birds he found the presence or absence of wing claws could not be looked upon as an ordinal, familial, generic, or even specific character in all cases. The apparent implication in the present record is that not only may vestigial wing claws appear occasionally in passerine birds, but that in this case the character may even have been an hereditary trait, inasmuch as it is present in each of three birds collected in one place, and is otherwise absent. It would seem hardly likely to be a mere accidental coincidence.

The claws are fairly straight, curved slightly terminally, measure 2.5–3.5 mm. in length, and lie flat, parallel to the alular quills. The large size of the claws (which was what made them conspicuous and thereby attracted attention) is brought out by comparing with the figures given by Fisher. They equal, or even exceed in size, claws recorded by him from various species of gulls.

The present note is written at the request of the collector, who is preparing a general report on his collection.—HERBERT FRIEDMANN, *United States National Museum, Washington, D. C.*

Genera of Birds Bearing Vestigial Claws on the Wings.—Fisher (Amer. Midl. Nat., 23 (1): 234–243, 1940) has summarized the known occurrence of claws on the digits of birds' wings. Wing claws have not been recorded by Fisher for the six genera listed below. Claws were noted in the genera listed while I was preparing skeletons for the scientific collections at the University of Michigan Museum of Zoology. All of the specimens listed in the table (except the two of *Buteo*) were

[1]Published by permission of the Secretary of the Smithsonian Institution.

received from the Detroit Zoological Park where they had been captives. In the specimens examined I found wing claws only on digit one. Unfortunately, I kept no detailed record of the condition of the claw; my notes merely indicate its presence or absence. However, in all of the genera listed, the claw was sufficiently well developed that it could be seen readily (after the feathers were parted or removed) without the use of optical aids.

Anatidae, *Coscoroba*, one adult.

Accipitridae, *Accipiter cooperii*, one fully-grown immature, and *Buteo jamaicensis*, two fully-grown immatures.

Gruidae, *Anthropoides virgo*, one adult, and *Balearica*, one adult.

Rallidae, *Laterallus leucopyrrhus*, one adult.—HARRISON B. TORDOFF, *Museum of Natural History, University of Kansas, Lawrence, Kansas.*

Captive Raven Carries Food to Non-captive Black Vulture.—During the week of February 4, 1951, the temperature in Washington, D. C., dropped to 14 degrees above zero F. The city and The National Zoological Park were covered with snow and a sheet of ice. During this cool weather a visitor to the Zoo informed me of the unusual behavior of a Northern Raven, *Corvus corax principalis*, and a Black Vulture, *Coragyps atratus*. The Raven is caged in a roomy outside enclosure and daily is given a varied mixture of food consisting of grain, boiled egg, mockingbird food, bread crumbs, and raw hamburger meat. The visitor informed me that he had seen the Raven pass out through the bars of the cage, a beak full of hamburger to a non-captive Black Vulture. Wishing to verify this observation, I stationed myself some 100 feet away to await developments.

I saw the Raven retrieve a hidden ball of meat and thrust it through the bars of the cage. Immediately a vulture dropped from a nearby tree and accepted the food from the beak of the Raven. The Raven walked away uttering a low guttural call.—MALCOLM DAVIS, *The National Zoological Park, Washington, D. C.*

The Number of Eggs Laid by the Passenger Pigeon, *Ectopistes migratorius*.—It has been customary to state that the Passenger Pigeon laid one or two eggs. For example, C. W. Townsend (*in* Bent, Bull. U. S. Natl. Mus., 162: 386, 1932) wrote: "The passenger pigeon laid either one or two eggs in a set, probably more often only one." There are three reasons for limiting the number to one: (1) Captives never laid more than one egg to a set; (2) Capable ornithologists never found in the wild more than one egg in a single nest, or small groups of nests, where the chances of two females laying in the same nest were reduced to a minimum in comparison with colonial nestings; and (3) The best evidence is biological. Mr. Willard informed Prof. C. F. Hodge (Forest and Stream, 74: 812, 1910) that in dressing thousands of wild birds for the market only a single developed egg was ever found. C. O. Whitman (Pigeons, 3: 6, 1919) found that five to eight days were required for the deposition of a second egg when the first was broken or removed.—A. W. SCHORGER, *168 N. Prospect Ave., Madison, Wisconsin.*

NOTES AND NEWS

Student Membership Awards for 1952 Selected by the A. O. U. Committee on Education

John Dietrich Battenberg, Carleton College, Northfield, Minnesota
Laurie Binford, New Trier Township High School, Winnetka, Illinois
Darl Eugene Bowers, University of California, Berkeley
Robert Irvin Bowman, University of California, Berkeley
Marjorie Ann Briggs, University of Florida, Gainesville
Joseph Carl Daniel, University of Colorado, Boulder
Stuart P. Davey, University of Michigan, Ann Arbor
Gerald Irving Day, University of Arizona, Tucson
Walter N. Gnann, Clemson College, Clemson, South Carolina
Donald Charles Goodman, University of Illinois, Urbana
(Mr.) Marion Lee Hundley, West Virginia University, Morgantown
Richard Allen Hunt, University of Wisconsin, Madison
Ned Keith Johnson, University of Nevada, Reno
Tom Kemper, Northwestern University, Evanston, Illinois
Merlin L. Killpack, Brigham Young University, Provo, Utah
Cecil Eugene Knoder, Ohio State University, Columbus
Richard W. Macomber, Northwestern University, Evanston, Illinois
Christopher Moore Packard, Bowdoin College, Brunswick, Maine
Thomas Matten Rycraft, San Jose State College, San Jose, California
John Breaks Scroggin, Texas A. and M. College, College Station
Robert L. Stephenson, University of Michigan, Ann Arbor
James M. Walters, University of California at Los Angeles
Franklin Elling Willis, University of Minnesota, Minneapolis

Annual Stated Meeting

The Seventieth Stated Meeting of the American Ornithologists' Union will be held at Baton Rouge, Louisiana, from October 20 through October 24. George H. Lowery, Jr. is Chairman of the Local Committee on Arrangements.

Zoological Record

The Aves section of Volume 86 (covering 1949) of the 'Zoological Record' has been issued recently, and may be ordered through the Treasurer, Dr. R. A. Moser, R. R. 1, Omaha 4, Nebraska. The cost of this new section is $1.10. To avoid errors in mailing, names and addresses should be printed clearly or typed.

Dues

Because of the equality of the Canadian and United States dollars, all Canadian remittances should be sent directly to the Treasurer, Dr. R. A. Moser.

'Systematic Zoology'

This new journal initiated by the Society of Systematic Zoology, will appear quarterly. Correspondence should be sent to Dr. R. E. Blackwelder, Rm. 429, United States National Museum, Washington 25, D. C.

RECENT LITERATURE

Beitrage zur Morphologie der Kiefermuskulatur der Oscines. Walter Fiedler. Zool. Jahrb. (Anatomie), 7: 235–288, 25 figs. 1951.—This important contribution to our understanding of the anatomy of passerine birds presents the results of an investigation of the extent to which jaw musculature in the Oscines conforms to a narrow basic pattern, despite observed adaptive differences in individual species. It thus forms a valuable addition to the careful studies of Moller on nectar-feeding birds, though it is more in the spirit of comparative anatomy than of functional anatomy. The species studied by Fiedler are: *Calcarius* sp., *Emberiza citrinella, Carduelis carduelis, Fringilla montifringilla, Pyrrhula pyrrhula, Pinicola enucleator, Loxia curvirostra, Coccothraustes coccothraustes, Munia oryzivora, Parus major, Parus cristatus, Panurus biarmicus, Paradoxornis* sp., *Sitta europaea, Certhia brachydactyla, Turdus musicus, Cinclus cinclus, Lanius senator, Nucifraga caryocatactes, Corvultur crassirostris, Hirundo rustica, Dryobates villosus, Micropus apus,* and *Falco peregrinus.* His comparison of his own studies on oscinine relationships with those of other authors for the non-passerine groups of the Coraciomorphae (Gadow's Second Legion) is particularly valuable. In the plan of his paper the description of the jaw musculature is followed by a section on innervation, then one on the ligaments of the jaw articulation. Finally he goes over the material again in a comparative section from which some details are drawn below.

The jaw musculature is supplied by the *Ramus mandibularis* of *N. trigeminus* and the *Ramus posterior* of *N. facialis.* The latter supplies *M. depressor mandibulae,* and the former innervates all the rest of the jaw musculature. Drawing on the unpublished findings of Feninger, Hofer, and others, as well as his own on Oscines, he gives an interesting account of the ligaments and patellae of the quadratomandibular joint. He found that all Oscines, except *Loxia,* have at least one patella in this position. Some have two, but this varies between species of a group, and he thinks on the basis of Hofer's study of *Uroaëtus* that dense connective tissue has often been mistaken for a patella.

In the comparative section he deals with the structural modifications noted in each of the muscle groups, both for the Oscines dissected by himself and for the representatives of other forms of Coraciomorphae dissected by other workers. He finds great constancy in the jaw muscles of passerines, contrary to findings in non-passerines. As regards *M. adductor mandibulae externus,* Hofer found that, within an order (Steganopodes, Gressores) some species may have a two-parted, others a three-parted muscle, whereas in Oscines it is always three-parted. Similarities in this muscle between the hummingbird *Sericotes* and the swift *Micropus* he assigns to close relationship despite different adaptation. Differences in this muscle in *Micropus, Hirundo,* and *Caprimulgus* (despite similar feeding adaptations) he thinks result from their membership in different groups. In *M. pseudotemporalis* he believes the one-parted condition primitive, the two-parted condition tending to be typical for passerines; and from the different emphasis on lateral or medial part he infers relationship. For finches the medial, for crows and shrikes the lateral slip, is seen to advance its insertion anteriorly along the median surface of the mandible with increased need for powerful adduction.

Fiedler discusses the relationships of two muscles originating on the quadrate. *M. quadratomandibularis* is missing in the parrots, Psittaci; its place is taken by the relatively weak *M. adductor posterior.* In the hornbills, Buceroti, the former is well-developed, the latter reduced. In the goatsucker *Caprimulgus, M. quadra-*

tomandibularis is missing entirely, as is the orbital process of the quadrate on which it has its attachment in forms in which it is present. In the swift *Micropus* and the hummingbird *Sericotes* the two muscles cannot be separated, whereas in the swallow *Hirundo* they are separated by a clear gap. In a series having similar feeding adaptations, he reasons that even the weak development in *Micropus* puts it in closer relationship to *Hirundo* than to *Caprimulgus* which lacks it altogether. Nevertheless, he concludes that this is not a good character for classification in non-passerines. Within the Steganopodes, *Phaëthon* and *Pelecanus* have it and *Sula* and *Phalacrocorax* lack it. Differences in *M. adductor posterior* in Oscines with increase in biting power are of degree, not kind, and the distinct presence of both muscles in all Oscines points up what he states repeatedly—that the muscle pattern in song birds is constant. There is no evidence of one muscle being replaced by another, as happens in non-passerines. Again, in *M. pterygoideus* he finds conformance to a single plan. He points out that, while the *M. pterygoideus dorsalis* has the rôle of drawing the upper mandible down, *M. pterygoideus ventralis* helps the adductors draw the lower mandible up, thus insuring co-ordination of the mandibles. The different balancing of these muscles against each other by the adaptive needs of the individual species accounts for the differences that exist. He discusses the asymmetry of these muscles in the crossbill, *Loxia*.

Fiedler compares the structure of specific muscles in titmice, finches, and shrikes, or within the Fringillidae, without regard to subgroups, even including the ploceid, *Munia*. One might wish for a greater awareness of current views of passerine classification—for example, that these finch groups have separate origins and have, therefore, achieved the adaptation for seeds independently. Unfamiliarity with ornithological literature is again suggested when he states his inability to discover the food habits of *Paradoxornis*. These can be found in the standard regional works covering its range. But he does not claim to study relationships and could not with his rather small sample—21 species of 11 families out of about 5000 species of 49 families (after Stresemann)—though one might expect a somewhat deeper study of function in view of his expressed interest in the adaptations.

Of course one of the deterrents to anatomical studies of passerine relationships is the large number of species to be dissected and classified. Various workers in different groups should be able to refer to Fiedler's drawings and thus avoid repeating his work, and for this his drawings should be as detailed as possible. He does not indicate either in text or drawings that the rostral slip of *M. adductor mandibulae externus* in *Lanius*, *Nucifraga*, *Parus*, *Munia*, and *Emberiza* is pinnate, a point important both to function and classification—but his illustrations are too small to indicate this had he wanted to.

He concludes that the material studied is too meager to permit the placement of disputed forms, but in groups of still undetermined homogeneity the muscle structure can clearly delimit the boundaries. It can also form the basis for deciding relationships between these groups. As an example, he would relate Fringillidae to Ploceidae, Laniidae to Corvidae, and Paridae to Paradoxornithidae. The reviewer agrees with the statement but not the example. Having only his sparse sample, Fiedler seems unaware of the danger of confusing convergent groups with phylogenetically related ones.

Finally, Fiedler departs radically from the nomenclature of Lakjer (1926), followed by Moller (1931), which was a careful attempt to stabilize terminology based on the homology of the jaw musculature for the entire Sauropsida. In his *M. adductor mandibulae internus* he includes Lakjer's *M. pseudotemporalis profundus*, *M. p.*

superficialis, and *M. pterygoideus* on the strength of an unpublished thesis by Feninger and of Hofer's (1950) work. He claims that Feninger's investigation of innervation shows the homogeneity of *M. adductor internus* and that this is supported by his own and by Hofer's studies. He also follows Hofer in changing *M. pseudotemporalis profundus* to *M. quadratomandibularis*, a term descriptive of its location in birds, because Hofer claims the homology of this muscle with the reptilian one is not established. In view of current studies (Straus, Biol. Rev., 21: 75–91, 1946) this claim receives some support. There is no doubt that Fiedler's nomenclature is simpler insofar as it is more descriptive of muscle position in birds, though one would be inclined to abandon Lakjer's attempts at stabilization of terminology only reluctantly.

This paper is reviewed rather critically because of the unfamiliarity of many ornithologists with this branch of study, but few of the points discussed seriously detract from Fiedler's work which is of very real value as a contribution in the field of the anatomy of passerine birds.—W. J. BEECHER.

A Guide to Bird Finding East of the Mississippi.—Olin Sewall Pettingill, Jr. (Oxford Univ. Press, New York), xvii + 659 pp., many ills. 1951. Price, $5.00. This book covers a new sector among field-guides. There are excellent guides to field identification of birds. It is logical to produce one which answers the question where and when can I find it? Other authors have had the idea, but Dr. Pettingill has had the persistence to carry the job through. It is an important contribution to ornithological field literature.

This volume covers states east of the Mississippi. A western volume is promised. The information is classified by states. Physiographic regions and types of habitats are described. There are lists of birds likely to be found in each.

To the growing thousands of bird watchers, this book with its mine of detailed information cannot fail to be of service. Obviously the local experts would be completely swamped if every bird watcher who came to town were to look them up. Dr. Pettingill's book will take a load from the shoulders of the generous but busy field naturalists in many communities.

The concentration points in the various states are well selected. Obviously, locations which shelter unusually rare or vanishing species ought not to be advertised in a guide of this kind. Dr. Pettingill has been aware of this. The lists of species given for most areas are usually, and very properly, of the more common birds. The more seasoned searchers for birds usually want to know of the rarer possibilities. But these seasoned observers usually become acquainted with the local experts who know of certain rarities which could not find a place in a formal guide to bird finding.

The author, with due regard to the location of the majority of bird people, heavily emphasizes the metropolitan areas and their immediate environments. Perhaps the weight of emphasis here could be somewhat modified in later editions, because most of the ornithological rarities are not to be found in city or suburban areas.

The author and his collaborators have consistently used great care in providing accurate information. One wonders, however, how soon rapidly changing conditions so characteristic of the United States, particularly in the East, the renumbering of route numbers, etc. will call for a new edition. Obviously a book of this kind, which is chiefly a travel guide, must be kept up to date if it is to continue to be of service. This point is recognized by the author in his preface, but it is important enough to bear emphasis.

To bird searchers who are fortunate enough to travel in quest of new species this guide will be of particular value in its coverage of states which are not so much on the

beaten track. The sections, for example, on New York, New Jersey, and Massachusetts, with their great squadrons of bird watchers, will not fill so great a need as the admirable chapters on Georgia, Alabama, and Mississippi.

There are no maps. Line maps in black and white would greatly enhance the usefulness of the book. To find out-of-the-way spots on the basis of word descriptions is notoriously difficult.

One of the most valuable features of the book is the full and careful index which makes it possible for the reader to look up the species in which he is interested, and find in the body of the book reference to the locations where they may be seen.

The line drawings by George Miksch Sutton scattered through the book are strong and clear, are treated with sensitive regard to page design, and add greatly to the pleasure of using the book.—GUY EMERSON.

Contributions to the Breeding Biology of *Larus argentatus* and *Larus fuscus*. Knud Paludan. (Ejnar Munksgaard, Copenhagen), 142 pp., 2 pls., 30 text-figs., 1951. Price, 20 kroner.—This study, reprinted from Vidensk. Medd. fra Dansk naturh. Foren., 114:1–128, 1951, is here issued as a separate work with a summary in Danish (pages 129–142). It is based on some six years of observation and study on the island group of Ertholmene, especially the island of Graesholm. In the spring, when the Herring Gulls first occupy the colony, their courtship is still incomplete and their gonads are small. Both developments show great acceleration in the week or two before the first eggs are laid. This "pre-egg stage" lasts from six to seven weeks, although in 1947 it was reduced to 16 days "which seems to be the minimum time in which the synchronization of the partners and the final growth of the gonads can take place." In *Larus argentatus* 25 per cent of the individuals begin egg-laying during the first week of the egg-laying period, while in *L. fuscus* it may not be until the third week of the egg-laying period that 25 per cent of the birds have started laying. Eggs are normally laid at intervals of 48 hours, and the interval between the destruction of a clutch and the commencement of repeat laying is 11–12 days in both species. If eggs are removed from the nest at the beginning of egg laying, a fourth egg is laid, but not if the eggs are removed later than 24 hours after the laying of the second egg. If the eggs are constantly removed immediately after each is laid, protracted laying will occur. Cessation of copulation and the onset of broodiness occur as a consequence of the bird's contact with the eggs and not as a consequence of the actual egg-laying process. In the area studied intensively, about 2.5 chicks hatched per pair of *L. argentatus* and not quite 2.0 per pair of *L. fuscus*. At most, 20 per cent of the *argentatus* chicks and 5 per cent of the *fuscus* chicks grew to be fully fledged. Statistical calculations from banding records indicate a mortality rate of about 15 per cent of the population of sexually mature birds. In order to maintain the population at an even status, from 0.5 to 1.0 chick per pair of adults is necessary. In the American breeding population figures the mortality rate is 29 per cent, which means that about three times as many chicks must survive in the American population as in the Danish.—HERBERT FRIEDMANN.

Migration of Birds. F. C. Lincoln. (Fish and Wildlife Service, U. S. Dept. Int.) Circular 16, pp. iii + 102, 23 figs., 1950. (For sale by Superintendent of Documents, Washington 25, D. C.; Price, 30 cents.)—Those who are familiar with the previous circular by Mr. Lincoln on the migration of North American birds (No. 363, October, 1935) will be pleased with the more attractive format of the present one. They will be disappointed, however, that there has been little revision of the older circular.

The circular begins with remarks on the mystery of migration and a brief account (pp. 4–10) of two theoretical aspects of migration—advantages of migration and origin of migration. Although it is readily apparent that migration seems advantageous, the theories presented to account for its origin cannot help but be confusing to a beginner. The northern and southern ancestral home theories are concerned primarily with defining the ancestral home from which birds migrated and are based on the assumption that migratory behavior is an hereditary habit. The theory of photoperiodism is concerned with the annual stimulus for migration and not with the place of origin of the ancestral stock. The final theory presented, the theory of continental drift, is concerned essentially with the evolution of migratory routes in certain species and not the origin of migratory behavior. In the opinion of the reviewer, a more general presentation of the fundamental problems of migration and the theories postulated under each would be more helpful to a beginner. The bulk of the book is concerned with the "mechanics" of migration—when, where, and how birds migrate (pp. 11–69). Much of the material presented in these pages is identical with that published in 1935. The figures have been redrawn by Bob Hines and are more attractive. Of the 23 figures, only four are new, those depicting the four flyways of North America. Of the 19 figures used in 1935 and 1950, 15 appeared also in 1915 in the circular on migration by Wells W. Cooke. No mention is made of the relation between the banding data and observations of the past 35 years and the original data which were used to illustrate the speed of migration. In the final pages there are brief discussions of such topics as: evolution of migratory routes, vertical and vagrant migration, perils of migration, influence of weather on migration, and problems of migration. There are two appendixes, a bibliography, and an index.

The stated purpose of the book is "a brief presentation of the facts on the migratory habits of birds scientifically gathered by the Fish and Wildlife Service over many years" for the use of bird-study classes, conservation organizations, farmers, and others interested in the welfare of birds and, especially, in regulatory action for the protection of birds. There is no doubt in the reviewer's mind that the author has succeeded in presenting some of the facts of migration in a readable, interesting, and attractive manner, and at a cost that makes the book available to everyone.

The serious amateur or interested student may get the impression from the date of publication, 1950, and the presentation of such recent studies as hibernation in the Poor-will, the theory of continental drift, the new recoveries of Arctic Terns, etc. that the book includes all of the significant studies prior to 1950. However, a careful comparison with the text and figures of 1935 reveals that little is new. Moreover, when one finds a phrase—"during the World War" in the 1935 edition revised to read "during the World Wars," in the 1950 edition, with no change in the text which follows, he cannot help but wonder about the accuracy of the revision. Errors in citation and in the bibliography, loose statements, and omission of significant facts detract from the value of the book to serious students, but it was, after all, not written for them.—ALBERT WOLFSON.

Where Birds Live: Habitats in the Middle Atlantic States. Edited by Shirley A. Briggs and Chandler S. Robbins. (Audubon Soc. Dist. Columbia, Inc.), pp. 1–58, 1 map, 15 drawings, 26 photos, 1951. Price $0.75.—Assembled as chapters of this paper-covered book are 12 papers by various authors that once appeared in the 'Atlantic Naturalist' (including its predecessor, 'The Wood Thrush'), the journal of the Audubon Society of the District of Columbia. The chapters cover, altogether, the principal avian environments of the Washington Region (*i.e.*, the District of Columbia, Maryland, Delaware, and the northeast third of Virginia) from

ocean and ocean beaches to pine and upland deciduous woods. Nearly all the environments are described to the extent of mentioning the dominant plants or other important factors directly influencing the presence of bird life. Considerable space in each chapter is devoted to the kinds of birds to be found at different seasons and their relative abundance. A few of the chapters go into greater detail than others by pointing out the vegetation types or the niches in which the birds may be looked for. Occasionally a specific locality for a particular environment is indicated. Since the primary purpose of the book is "to assist bird watchers who are beginning to get acquainted with the birds of the Washington Region," it would have been helpful if a little more space had been taken to give specific localities for all the environments, together with directions for reaching them.—OLIN SEWALL PETTINGILL, JR.

Fauna of Thailand. Chote Suvatti. (Dept. Fisheries, Bangkok), pp. ii + 1100, frontispiece, 1950.—This pretentious publication purports to list all animal forms reported from Siam in the world's scientific literature, and to give a complete bibliography of sources, by chronology, by phyla, and by authors. The Class Aves is treated on pages 603 to 654, where the names of 230 forms are given, without the least attempt to collate synonyms.

Inasmuch as the entire work is straightforward compilation, the results are not nearly good enough, especially when it is considered that the undersigned has reported, in a single volume available to Suvatti, more than 600 different birds from northern Thailand alone, and that his personal files of *published* records of Siamese birds are divided among considerably more than 1,000. The value of this egregious book may be fairly summed up by noting that but two names appear under Timaliidae, and but three under Muscicapidae (of which the first and second are synonymous)!

There is no reason to suppose that the lists of names of groups other than birds are more soundly constructed, and one can only deplore the volume's publication as a waste of public funds.—H. G. DEIGNAN.

ABDULALI, HUMAYUN. 1951. Extension of breeding range of the stilt (*Himantopus h. himantopus*), and some notes on its habits and plumages. Journ. Bombay Nat. Hist. Soc., **49** (4): 789–791.

ALCORN, J. R., AND FRANK RICHARDSON. 1951. The Chukar Partridge in Nevada. Journ. Wildl. Manag., **15** (3): 265–275.—*Alectoris graeca chukar* is now well established in western Nevada after liberations which began in 1934. Late summer and early fall foods include seeds of *Bromus tectorum* and *Erodium cicutarium*, leaves of *Poa secunda*, and grasshoppers. Fourteen clutches averaged about nine eggs. In summer, the birds are restricted to vicinity of water; in winter they move to higher, wind-blown areas. "Males tend to band together while the females are nesting."—J. J. HICKEY.

ALEXANDER, H. G. 1951. Some notes on birds in Lahul. Journ. Bombay Nat. Hist. Soc., **49** (4): 608–613, 1 sketch-map.—Observations made between June 16 and June 30, 1950, supplementing and confirming those made by the late Hugh Whistler in 1921, 1922, and 1923 (Ibis, 1925: 152–208).—H. G. DEIGNAN.

ALI, SÁLIM. 1951. The Heart-spotted Woodpecker—*Hemicircus canente*. Journ. Bombay Nat. Hist. Soc., **49** (4): 786–787.—The species is shown to have a continuous range and to exhibit a gradual cline in size from southwestern to northeastern India. Since it is not possible to define exact geographical limits for either of the two commonly accepted races, it is suggested that the subspecies *cordatus* be suppressed.—H. G. DEIGNAN.

ALI, SÁLIM. 1951. White-bellied Drongo catching a bird. Journ. Bombay Nat. Hist. Soc., **49** (4): 786.—*Dicrurus caerulescens* was seen to capture a wren-warbler (*Prinia*) in mid-air.

AUSTIN, O. L., JR. 1951. The Mourning Dove on Cape Cod. Bird-Banding, **22** (4): 149–174.—This study is based on 2,690 *Zenaidura macroura* banded from 1930 to 1950. Because of over-shooting, this bird had become rare in New England by 1900; after complete protection given in 1908 in Massachusetts it became a common summer resident on the Cape by the 1920's and has remained so ever since. A map shows the recoveries in the southern coastal plain. Annual mortality, starting from fledging, is about 80% the first year and 55% for the next 10 years. No observations were made on nesting, but the author calculates that 4.6 young per pair must be fledged each season to keep up the population. This requires "a nesting success of 77%" in three broods of two eggs each. Such a figure is out of line with the less than 50% success of eggs laid found in other published nesting studies on this species, as well as in studies of other altricial species with open nests, which showed about 45%; and it is even higher than the 66% success of hole-nesting species. McClure (Auk, 63: 26, 1946) reported 46.6% success with 8,018 Mourning Dove eggs. Mourning Doves may attempt more than three broods. McClure (Bull. Iowa State Coll., 310:384, 1943) found that 772 pairs in 3 years averaged 4.6, 5.1, and 5.4 attempts to nest per season. Five sets of 2 eggs equal 10 eggs and 46.6% success would give 4.66 young fledged per pair. Thus, doves may not require 77% success in all instances to keep up the population.—MARGARET M. NICE.

AUSTIN, O. L., SR. 1951. Age record for the Arctic Tern. Bird-Banding, **22** (4): 179.—An adult *Sterna paradisaea*, banded June 29, 1929, on Cape Cod, was retaken in 1936 and 1946 and found dead at Tern Island on July 13, 1951, "at least 23 years old, probably more," as this species usually starts breeding at three years of age.

BEECHER, WILLIAM J. 1951. A possible navigation sense in the ear of birds. Amer. Midl. Nat., **46** (2): 367–384, 8 figs.—In a critical review of the structure of the avian ear the author attempts to assign functions in navigation. The idea that movements of air in the tympanic cavity make the bird aware of thrusting movements of the head is new. If the head is maintained in its usual position the semicircular canals and otolith structures are inactive. Any streaming of the endolymph in the canals, as a result of the Coriolis force when the head is moved laterally, might provide a sort of compass for navigation.—H. I. FISHER.

BEHLE, WILLIAM H., AND ROBERT K. SELANDER. 1951. The systematic relationships of the Fox Sparrows (*Passerella iliaca*) of the Wasatch Mountains, Utah, and the Great Basin. Journ. Wash. Acad. Sci., **41** (11): 364–367.—Description of *Passerella iliaca swarthi* (North Fork, Ogden River, 5,200 ft., 2 miles west of Eden, Weber County, Utah).

BELLROSE, FRANK C. 1951. Effects of ingested lead shot upon waterfowl populations. Trans. 16th N. A. Wildl. Conf., pp. 125–135.—Of 4561 live-trapped Mallards in Illinois, 7.7 per cent carried ingested shot. Regionally this runs about 5.1–7.7, except in the Great Plains (2.7 per cent), and is 6.57 per cent for 18,454 ducks of all species. Banding results show that the number of pellets ingested is inversely correlated with the rate of movement by ducks and directly with the percentage of total bands returned.—J. J. HICKEY.

BENSON, C. W. 1948. Evergreen forests near Blantyre. Comparative variety of bird species. Nyasaland Journ., **1** (2): 45–53.—The bird life of the isolated small

highland forests on the hills within 25 miles of Blantyre suggests that these sylvan areas were at one time linked together. The variety of birds inhabiting each of them today varies directly with the size of the individual forest area.

BENSON, C. W. 1951. A roosting site of the Eastern Red-footed Falcon, *Falco amurensis*. Ibis, **93** (3): 467–468.—Several thousand of these winter visitors from northeastern Asia roosted in a grove of large trees near Dedza, Nyasaland.

BENSON, C. W. 1951. The bird life of Lake Nyasa. Nyasaland Journ., **4** (2): 40–66.—A rough ecological summary of the birdlife of the lake and its immediate environs.

BERGMAN, G. 1951. Unterschiede von Silbermoewe (*Larus a. argentatus*) und Heringsmoewe (*Larus f. fuscus*) in Lebensweise und Stimme. Vogelwarte, **16**: 17–18.—Differences in behavior, migration, situation of nesting colonies, molt, start of breeding season, size of colonies, food, and voice between Herring Gull and Lesser Black-backed Gull.

BISWAS, BISWAMOY. 1951. A new race of the ground-thrush *Turdus citrinus* (Aves: Turdidae). Journ. Bombay Nat. Hist. Soc., **49** (4): 661–662.—*Turdus citrinus amadoni* (Chanda, Chanda District, Central Provinces, India).

BRADT, GEORGE M. 1951. Birds of prey—do they deserve extinction? Desert Mag., **14** (13): 21–23.—Pictures of Swainson's Hawk, Golden Eagle, and Burrowing Owls.

BRENNECKE, H. E. 1951. Zur Jagdweise des Merlin-Falken. Vogelwelt, **72**: 82–84.—Description of the various methods by which Pigeon Hawks take their prey.

BROWN, R. H. J. 1951. Flapping flight. Ibis, **93** (3): 333–359.—Review of previous work on anatomy and wing motion with an attempt at a physical interpretation of wing shapes. There is an inconclusive account of the energetics of flight and a statement of some elementary notions of aerodynamics.—C. H. BLAKE.

BRUNS, H. 1951. Wann werden hartschalige Insekteneier von Meisen gefressen? Ornith. Mitt., **3**: 59–61.—Titmice (*Parus*) ignore most hard-shelled insect eggs.

BUMP, GARDINER. 1951. Game introductions—when, where and how. Trans. 16th N. A. Wildl. Conf., pp. 316–325.—A progress report on the introduction of exotics by the U. S. Fish and Wildlife Service. "The world game bank contains at least 355 species and 678 subspecies" of megapodes, guans, grouse, Phasianinae, guinea fowls, "Sand Grouse," bustards, and tinamous—"still largely unexplored resources to fill out vacant habitats." Climacurves are described by which monthly minimum and maximum temperatures can be used to analyze climatic factors; a six-point plan of study is described.—J. J. HICKEY.

CARL, G. CLIFFORD, C. J. GUIGET, and GEORGE A. HARDY. 1951. Biology of the Scott Island Group, British Columbia. Rept. Prov. Mus. Nat. Hist. and Anthrop., 1950: B21–B63, 17 figs.—Includes annotated lists of birds observed during visits to these islands in June, 1949 and 1950. The Group lies west of the northern tip of Vancouver Island.

CEYLON, NATIONAL MUSEUM OF. 1951. Administration report of the director . . . for 1950. Ceylon Admin. Rept. [Part IV—Ed., Sci. and Art (E)].—On page E 14 of this document, issued on June 12, 1951, P. E. P. Deraniyagala gives a valid description of *Eurystomus orientalis irisi* ("its skull is narrower and its wing length averages 183 mm. whereas in the Travancore race it is 200 mm."), based upon one male and one female from Maha-oya, Ceylon. A crude colored plate is inserted as a loose extra sheet. The author promises to discuss the bird in a future number of 'Spolia Zeylanica,' and gives no explanation for his eccentric choice of a medium for first publication!—H. G. DEIGNAN.

CLANCEY, P. A. 1951. The characters of a new race of Lanius collurio L from the western Palearctic Region. Bonner Zool. Beitr., **2** (1–2): 83–84.—*Lanius collurio juxtus*, from Martlesham, Woodbridge, East Suffolk, England.

COLE, LAMONT C. 1951. Population cycles and random oscillations. Journ. Wildl. Manag., **15** (3): 233–252.—Peaks of *Perdix perdix* harvested in England, as well as certain other cyclic phenomena, are shown to have a mean length of 3.0–5.8 years and a coefficient of variation of 27.1–50.1 per cent, whereas peaks in Tippett's random numbers average 2.9 "years" apart, with a V of 33.2 per cent. Thus, short-term cycles may well originate from such data, if peaks are recognized only when they reach some fixed proportion (such as 89 per cent) of the maximum value attainable. No explanation of the synchronism in grouse cycles is offered. —J. J. HICKEY.

COLLIAS, NICHOLAS E., AND RICHARD D. TABER. 1951. A field study of some grouping and dominance relations in Ring-necked Pheasants. Condor, **53** (6): 265–275.—Discussion of social organization during late winter and early spring (1947–48) of a wild population studied in a marsh near Madison, Wisconsin, where 38 cocks and 170 hens were trapped, color marked, and released. In winter the birds formed harems of hens, each harem under a single cock. Cocks dominated hens. In flocks at feeding stations dominance order was related to food competition and during the breeding season to crowing and establishment of territories.

COLLINS, HENRY H., JR. 1951. Birds of Montezuma Castle and Tuzigoot National Monuments. Illustrated by Roger Tory Peterson. (SW Monuments Assoc., Santa Fe, New Mexico), pp. 1–14, 7 col. pls., many other figs. Price, $0.25.—This attractive pamphlet is directed toward the park visitor who has a "potential" rather than a "developed" interest in nature. It is the first of a proposed series planned for various national parks and monuments.

COLLS, D. G. 1951. The conflict between waterfowl and agriculture. Trans. 16th N. A. Wildl. Conf., pp. 89–93.—As farming encroaches on ancient waterfowl areas, barley, wheat, oats, and peas are being more acutely damaged by ducks, especially Mallards and Pintails.

COMMITTEE ON BIRD SANCTUARIES IN THE ROYAL PARKS (ENGLAND AND WALES). 1950. Bird life in the Royal Parks. (Ministry of Works, London), pp. i–vi, 1–45, 1951. Price, 2 shillings.

COTTAM, CLARENCE. 1951. Waterfowl's future depends upon management. Trans. 16th N. A. Wildl. Conf., pp. 109–117.—Habitat development and restoration of breeding and wintering areas are a necessity. Refuges serve as insurance. Public hunting areas should be developed by the states in areas near large federal refuges. Restriction of the harvest by "flyways" is biologically sound and administratively necessary.—J. J. HICKEY.

DAVIDSON, A. 1951. Studies of some species rarely photographed. XXXIII. The Rustic Bunting. The Pine Grosbeak. Brit. Birds, **44** (10): 346–348.—Five plates of *Emberiza rustica* and *Pinicola enucleator* at nests in North Finland.

DEIGNAN, H. G. 1951. A new blackbird (Aves) from western China. Proc. Biol. Soc. Wash., **64**: 135.—*Turdus merula sowerbyi* (Loshan, Szechwan Province, China).

DEIGNAN, H. G. 1951. New passerine birds from the Indo-Chinese subregion. Postilla [Yale Peabody Mus. Nat. Hist.], No. **7**: 1–4.—*Pellorneum ruficeps vocale* (Kanglatongbi, elev. 2933 ft., Chief Commissioner's District of Manipur, India) and *Oligura castaneo-coronata ripleyi* (Likiang Mountains, Yunnan Province, China) are described. *Oligura* Hodgson, 1845, is shown to be a valid generic name, and *Chlorotesia* Delacour, 1942, is consigned to its synonymy.

DELACOUR, JEAN. 1951. Preliminary notes on the taxonomy of Canada Geese, *Branta canadensis*. Amer. Mus. Novit., No. **1537**: 1–10.—A brief review of geographical variation in the Canada Goose, based in part upon notes left by the late James Moffitt. Twelve subspecies are recognized, of which three are new: *B. c. maxima* from Round Lake, Grant Co., Minn. (this race is considered extinct); *B. c. taverneri* from Colusa, California (breeds in the interior of northern and northwestern Alaska); and *B. c. fulva* from Graham Island, Queen Charlotte Islands. The small, coastal, arctic Cackling and Hutchins's geese are considered to belong to the same species as the Canada Goose, since they appear to intergrade with it in some areas, though not everywhere.—DEAN AMADON.

DERANIYAGALA, P. E. P. 1951. see Ceylon, National Museum of.

DE SCHAUENSEE, RODOLPHE M. 1950–51. The birds of the Republic of Colombia. Their distribution and keys for their identification (cont.). (Reprinted in book form, Acad. Nat. Sci. Phila.). Caldasia, **5** (24): 645–871, 1950, and **5** (25): 873–1112, 1951.—This volume represents the conclusion of the main list of birds; previous installments were printed in Vol. 5, Nos. 22 and 23 of 'Caldasia,' 1948 and 1949.

EICHLER, WOLFDIETRICH. 1951. Mallophagen—Synopsis. XVII. Genus *Koeninirmus*. Bonner Zool. Beitr., **2** (1–2): 125–134, 6 figs.—Review of this genus of external parasites of birds.

ERICKSON, ARNOLD B., DAVID B. VESALL, C. EDWARD CARLSON, AND CLAIR T. ROLLINGS. 1951. Minnesota's most important game bird—the Pheasant. Flicker, **23** (3): 23–49, 9 figs., 6 tables.—Nest, foods, sex ratios, weights, parasites, behavior, mortality, and restocking and releasing of pheasants—based on a 10-year study.

FLEAY, DAVID. 1951. A Wedge-tailed Eagle for Christmas. 1951. Animal Kingdom, **54** (6): 162–169, 188–189, 8 photos.—Life history notes based on captive birds.

FREITAG, F. 1951. Am Nest des Rotkopfwürgers. Vogelwelt, **72**: 145–148.—Studies on nests of *Lanius senator*. Nest building continues after first eggs are laid; incubation period is 15–18 days.

GABRIELSON, IRA N., AND FREDERICK C. LINCOLN. 1951. A new Alaskan race of the Winter Wren. Proc. Biol. Soc. Wash., **64**: 73.—*Trogolodytes* [sic] *trogloydtes* [sic] *seguamensis* (Seguam Island, Aleutian Islands).

GABRIELSON, IRA N., AND FREDERICK C. LINCOLN. 1951. Post-mortem color change in bird specimens. Condor, **53** (6): 298–299.—Comparison of series of recently collected Fox Sparrows from Alaska with others taken at the same localities and seasons 50 years earlier showed that the latter had foxed and showed increased redness. Other species do not show so marked a change.

GABRIELSON, IRA N., AND BRUCE WRIGHT. 1951. Notes on the birds of the Fort Chimo, Ungava District. Can. Field-Nat., **65** (4): 127–140, 3 figs.—District visited in August, 1948. Comparisons with findings of Turner in 1882–1884 and Hildebrand in 1947–1948. Annotated list.

GIBSON, J. A. 1951. The breeding distribution, population and history of the birds of Ailsa Craig. Scot. Nat., **63** (2): 73–100, 7 figs., 2 tables.

GRANT, C. H. B., AND C. W. MACKWORTH-PRAED. 1951. Notes on East African Birds. Bull. Brit. Orn. Club, **71** (6): 38.—*Cyanomitra olivacea chyulu* van Someren = *C. o. neglecta* Neumann; *Cryptospiza salvadorii chyuluensis* van Someren = *C. s. kilimensis* Sclater; *Spinus citrinelloides chyulu* van Someren = *S. c. hypostictus* Reichenow.

GRIEB, JACK R. 1951. Tally counter holder for making field observations. Journ. Wildl. Manag., **15** (3): 334–335.—A wooden holder can be used to house three separate tally counters and thus simplify counting for some field investigators.

GUNN, W. W. H. 1951. The changing status of the Red-necked Grebe in southern Ontario. Can. Field-Nat., **65** (4): 143–145, 1 table.—Now a regular breeder in small numbers, and locally common in late summer and autumn along north shore of Lake Ontario.

HACHISUKA, MASAUJI. 1950. The occurrence of some rare Japanese birds. Tori, **13** (60): 21–24, 2 figs.—In Japanese. Includes records of *Turdus celaenops*, *Branta b. nigricans*, and *Tadorna tadorna*.

HAGEN, YNGVAR. 1950. Noen Iakttagelser over Hubro (*Bubo bubo* L.) I Rogaland. Stavanger Mus. Arbok, **1950**: 93–110, 8 figs.—Detailed life history based on four nests in Rogaland, Norway.

HAMILTON, W. J., JR. 1951. The food of the opossum in New York State. Journ. Wildl. Manag., **15** (3): 258–264.—Birds are prominent in the food items: robin, crow, "Meadow-lark," Bronzed Grackle and Vesper Sparrow. As in many other recent articles of this journal, scientific names of a number of animals are notably absent.—J. J. HICKEY.

HARPER, HAROLD T., CHESTER M. HART, AND DALE E. SHAFFER. 1951. Effects of hunting pressure and game-farm stocking on Pheasant populations in the Sacramento Valley, California, 1946–1949. Calif. Fish and Game, **37** (2): 141–176.—A harvest of 81–84 per cent of game farm birds was effected when the release was made two days before the hunting season opened. Stocking failed to increase breeding populations. In midfall, banded adults had bursae of Fabricius measuring 6–19 mm.—J. J. HICKEY.

HARTESVELDT, RICHARD J. 1951. The effect of climate on Pheasant range in Hawaii. Journ. Wildl. Manag., **15** (3): 330–332.

HARTESVELDT, RICHARD J. 1951. Sport for Pheasants? Journ. Wildl. Manag., **15** (3): 332.—Male Ring-necked Pheasants repeatedly glided down into the crater of an extinct volcano.

HICKEY, JOSEPH J. 1951. Mortality records as indices of migration in the Mallard. Condor, **53** (6): 284–297.—A review of over 6800 autumnal recoveries of banded Mallards in North America. Criticism of the duck-hunting pressure index based on the number of duck stamps annually sold.

HINDE, R. A. 1951. Further report on the inland migration of waders and terns. Brit. Birds, **44** (10): 329–346.—Charts are given showing the "Relation between the 18.00 hours temperatures at Bordeaux, Corunna, and Lisbon, and the passage of waves of migrants through the British Isles" from April 18 through May from 1947 through 1950. Such waves "usually coincide with, or follow, periods of warm temperatures in the Bay of Biscay area." "Winds are primarily of importance in that they may affect track or ground speed."—MARGARET M. NICE.

HÖHN, E. O., AND D. L. ROBINSON. 1951. Some supplementary bird notes from the general area of the Mackenzie Delta and Great Slave Lake. Can. Field-Nat., **65** (3): 115–118, 1 table.—Includes spring arrival dates in 1948 and 1949 for 23 species at Tuktoyaktuk, Mackenzie Delta.

HOLGERSEN, HOLGER. 1950. Sjøfuglundersøkelser I Rogaland 1949–1950. Stavanger Mus. Arbok, **1950**: 61–76, 7 figs.—Breeding birds and census of island of Rott, southwestern Norway.

HOLGERSEN, HOLGER. 1950. Stavanger Museums Ringmerkingsarbeid 1950.

Stavanger Mus. Arbok, **1950**: 77–86, 2 figs.—Brief accounts of significant recoveries of birds banded at the Museum.

HOLLOM, P. A. D. 1951. Great Crested Grebe sample census: report to end of 1950. Brit. Birds, **44** (11): 361–369.—Adult *Podiceps cristatus* have been counted in May and June in 21 counties in England for 6 years. The estimated totals were 1,760 in 1931; 1,445 in 1947 (after a very hard winter); 1,734 in 1948; and 2,178 in 1950. The grebes are attracted to "relatively newly filled waters."

HUBBS, EARL L. 1951. Food habits of feral house cats in the Sacramento Valley. Calif. Fish and Game, **37** (2): 177–189.—Of 184 stomachs containing food, 74 included bird remains. The 33 Pheasants and 10 ducks (mostly adult females), 8 Coots, 1 California Quail, 1 Domestic Chicken, 1 Green Heron, and 29 passerines found accounted for 25.2 per cent of the bulk.

HUBER, J. 1951. Einige brutbiologische Mitteilungen über den Flamingo. Vogelwelt, **72**: 73–77.—Description of a visit in 1948 to the flamingo colony in the Camargue. An estimated 6000 birds were nesting at the time.

HUNGERFORD, K. E. 1951. Ruffed Grouse populations and cover use in northern Idaho. Trans. 16th N. A. Wildl. Conf., pp. 216–224.—Annual fall censuses on 2200 acres ran 14.3, 15.1, 21.3, 14.3, and 11.1 birds per 100 acres, according to King's method. [Hayne's criticism of this technique seems to have been overlooked.] Hunting seasons of 2.5–3.0 days harvested 6.0–7.0 per cent of the total population. Microclimates on ridges and in ravines are importantly utilized by the birds according to season.—J. J. HICKEY.

HUXLEY, JULIAN. 1951. Natural history in Iceland. Smiths. Rept. for 1950: 327–338, 4 figs., 1 table.—Emphasis is on birds, with notes on life habits and changing populations.

INORUYE, MOTONORI. 1950. An examination of the food habits of birds as viewed from the control of may beetles. Tori, **13** (60): 9–21, 60.—Tabulated results (page 60) for many species. In Japanese with English summary. Birds do exert a suppressing effect on the insects in this region.

JANY, E. 1951. Der Balzruf eines südafrikanischen Ziegenmelkers. Vogelwelt, **72**: 157–160.—Observations of the calls of *Caprimulgus rufigena* made near Windhoek (S. W. Africa).

JOUANIN, CHRISTIAN. 1950. Catalogue systématique des types de Trochilidés du Muséum de Paris. Bull. Mus. Natl. d'Hist. Nat. Paris, Series 2, 22 (suppl. 11): 1–27.

JUDD, W. W. 1951. Bird lice (Mallophaga) from a Florida Gallinule and a Baird's Sandpiper. Can. Field-Nat., **65** (3): 120.

KARTMAN, LEO. 1951. Notes on *Tetrameres* sp. (Nematoda, Spiruroidea) parasitic in the English Sparrow in Hawaii. Pacific Sci., **5** (3): 252–255, 1 fig., 4 tables.

KEELER, J. E., AND F. WINSTON. 1951. Mourning Dove trapping in the Southeast. A cooperative dove study. Bird-Banding, **22** (4): 174–179.—A description of technique.

KIPP, FRIEDRICH A. 1951. Der Fischadler Süd-Chinas: *Pandion haliaetus mutuus* subsp. nov. Bonner Zool. Beitr., **2** (1–2): 112.—From Foochow, China.

KOSSACK, CHARLES W. 1951. Securing celluloid bands on waterfowl. Journ. Wildl. Manag., **15** (3): 335–336.—Sealing pliers can be used to fasten hollow rivets.

KUNO, KENTARO. 1950. Adaptability of the lark and the Great Reed-Warbler to their different habitats. Tori, **13** (60): 24–33.—Larks live successfully in areas of grassland as small as 50,000 square meters. Populations in this type of grass

(seasonally inundated) were as great as in adjoining dry land. The Reed-warbler will nest in dry bamboo forest if its usual habitat of reeds disappears. In Japanese.

KURODA, YASUKICHI. 1950. Notes on the moults and movements of the Korean Ring-necked Pheasants, Phasianus c. karpowi. Tori, **13** (60): 33–37.—Cocks molt early in fall and move into hills; females and young molt later. Females in winter are found chiefly in deciduous forest and males in mixed deciduous and coniferous forests. Local movements occur in relation to harvesting of crops. In Japanese with English summary.

LEITCH, WILLIAM G. 1951. Saving, maintaining, and developing waterfowl habitat in western Canada. Trans. 16th N. A. Wildl. Conf., pp. 94–99.—Efforts of Ducks Unlimited (Canada).

LISTER, M. D. 1951. Some bird associations of Bengal. Journ. Bombay Nat. Hist. Soc., **49** (4): 695–728, 1 sketch map.—A classification of cover types in the vicinities of Jessore, a country town, and Dhubalia, a smaller community, and discussion of habitat preferences exhibited by members of the local avifaunas.

LISTER, ROBERT. 1951. Trumpeter Swans breeding in the Cypress Hills of Alberta. Can. Field-Nat., **65** (4): 157–158.

LOCKLEY, R. M., AND S. MARCHANT. 1951. A midsummer visit to Rockall. Brit. Birds, **44** (11): 373–383.

LÖHRL, H. 1951. Brutbeginn und Entwicklung im Vogelei. Vogelwelt, **72**: 1–4.—The true incubation period is the time interval between the laying and hatching of the last egg. Earlier eggs, incubated only intermittently, usually hatch with the last egg or only slightly earlier. This may be due to two reasons—either a full 24-hour period of incubation is needed to initiate the development of the embryo or the brood patch does not start to function properly until the last egg is laid. Illustrated by case histories in *Muscicapa albicollis*.—E. MAYR.

LORENZ, K. 1951. Ueber die Entstehung ausloesender "Zeremonien." Vogelwarte, **16**: 9–13.—"Formalized" or "ritualized" actions may acquire a genetic basis and become specifically orientated. For instance, the "inciting" of the female duck, which in the Tadornini is still clearly composed of two components, a movement directed to the enemy and one directed to the male, has become a single rigid behavior pattern in the Anatini. While an "Uebersprungsbewegung" leads to nervous relaxation, the new instinctive pattern replacing it leads to nervous stimulation.—E. MAYR.

MACGREGOR, WALLACE, JR., AND MANLEY INLAY. 1951. Observations on failure of Gambel Quail to breed. Calif. Fish and Game, **37** (2): 218–219. *Lophortyx gambelii* remained in nonbreeding coveys during a drought, and delayed breeding for four months.

MANGOLD, R. E. 1951. Notes on Bob-white fall and winter mortality. Iowa Bird Life, **21** (3): 46–49, 3 figs.

MANVILLE, RICHARD H. 1951. A small island community in midsummer. Ecology, **32** (4): 608–617.—Eighteen pairs of breeding birds of 10 species on 9.5 acres of white cedar, aspen, and balsam fir; Michigan.

MARTIN, ALEXANDER C. 1951. Identifying pondweed seeds eaten by ducks. Journ. Wildl. Manag., **15** (3): 253–258.—*Potamogeton* seeds can be sectioned and identified under low-power magnification. Comments and illustrations on 21 species are given.

MCCLURE, H. ELLIOTT. 1951. An analysis of animal victims on Nebraska's highways. Journ. Wildl. Manag., **15** (4): 410–420.—Birds represented 23.5 per cent of 6723 animals counted in 3.3 years on 77,000 miles of road. Included were 17

Sparrow Hawks, 386 Pheasants, 55 Mourning Doves (mainly in July), 93 Burrowing Owls (especially in August), 109 Horned Larks, and 265 House Sparrows (mostly in July).

MEINERTZHAGEN, R. 1951. Some relationships between African, Oriental, and Palaearctic genera and species, with a review of the genus Monticola. Ibis, **93** (3): 443–459.—In the first portions of his article Col. Meinertzhagen sets up four categories: (1) The distributional gap between certain European species and their representatives in East Asia and North America; (2) The distributional gap between certain Palaearctic genera and species and their representatives in South Africa; (3) The close connection of certain South Asiatic genera and species with their representatives in Africa; and (4) The many more cases of true geographical races of Palaearctic birds in Africa than is generally realized. Numerous instances are cited under each heading, and in all such instances the "representative form" is relegated to subspecific standing. In many cases the author is doubtless correct, but in other instances the "theory of descent with modification" is applied too rigidly. For instance, Col. Meinertzhagen would place the true bitterns (*Botaurus*) in a single species, and thus the North American, South American, and Australian birds would all become races of the Palaearctic *B. stellaris*. These species, however, are not only widely separated in space, but probably also in time. It is entirely conceivable that they have developed different genetic characters which would render them reproductively isolated were they to be brought together. Under these circumstances they would be regarded as species under modern specific concepts. The types of representative forms are so diverse as to require a certain flexibility in the application of the "Formenkreis" theory.

The second portion of the article is devoted to a revision of the rock thrushes and of the genus *Monticola*, which embodies a mixture of the four categories already set forth. Four species are recognized (as against ten of all other authors) together with their respective races. The wide distributional gaps are emphasized and hypotheses suggested to explain these gaps.—J. L. PETERS.

MEISE, WILHELM. 1951. Hampes Mischzucht von Haus- und Feldsperling. *Passer d. domesticus* (L.) × *P. m. montanus* (L.). Bonner Zool. Beitr., **2** (1–2): 85–98.—Natural history, behavior, and development of these hybrids.

MEUNIER, K. 1951. Korrelation und Umkonstrucktion in den Grossenbeziehungen zwischen Vogelflugel und Vogelkorper. Biol. Generalis, **19** (4): 403–443.

MICHENER, JOSEPHINE R. 1951. Territorial behavior and age composition in a population of Mockingbirds at a feeding station. Condor, **53** (6): 276–283.—A sequel to an earlier paper, this describes modified behavior resulting from an unusual concentration of food provided at a feeding station at Pasadena from 1936 to 1940. The proportion of adults to juveniles increased. Mockingbirds may reach an age of at least 12 years.

MILLS, HARLOW B. 1951. Facts and waterfowl. Trans. 16th N. A. Wildl. Conf., pp. 103–109.—A plea for more research.

MOLTONI, EDGARDO. 1951. Brevi cenni sul parassitismo degli uccelli. Riv. Ital. Ornit., **21** (4): 129–136.

MOREAU, R. E. 1951. Geographical variation and plumage sequence in Pogonocichla. Ibis, **93** (3): 383–401, pl. (map).—This monotypic genus of African Turdidae is confined to the evergreen forests of eastern Africa; nine races are recognized and their characters graphically shown by means of five tables. A peculiarity of this species is the occurrence of three distinct plumages which appear to correspond to the juvenal, immature, and adult, but their sequence varies

geographically. In the southern population the olive (immature) plumage is regularly acquired, and it is believed that the birds may breed in that dress; in the northern groups young in the spangled (juvenal) plumage usually molt directly into the adult livery, but cases of progressive or retarded second (immature) plumages are common.—J. L. PETERS.

MURPHY, JOHN A. 1951. The nesting of the Black Swift. Nat. Hist., **60** (10): 446–449, 6 photos.—Popular account of first recorded nest of this species in Colorado.

NIETHAMMER, GÜNTHER. 1951. Arealveränderungen und Bestandsschwankungen mitteleuropäischer Vögel. Bonner Zool. Beitr., **21** (1–2): 17–54.—A comprehensive review of changes in status of Middle European birds, with accounts of invasions by breeding and non-breeding birds from other parts of the continent.

NORTH, M. E. W. 1951. Opportunism in the use of burnt ground for breeding. Ibis, **93** (3): 466–467.

NORTH, M. E. W. 1951. Tropic-birds at Ras Hafun. Ibis, **93** (3): 466.—Believes that a record of a probable breeding colony of Tropic-birds (Ibis, 1951:142) at Ras Hafun, Somaliland, is erroneous; that the previous author mistook a migrating flock for resident birds.

OWEN, D. F. 1951. Nightjars mobbing owls. Brit. Birds, **44** (9): 324.—Nesting pairs of *Caprimulgus europaeus* mobbed a Tawny Owl, *Strix aluco*, and Little Owl, *Athene noctua*.

PARKS, G. H. 1951. An old White-breasted Nuthatch. Bird-Banding, **22** (4): 180.—An adult male *Sitta c. carolinensis* banded Nov. 15, 1942, in Connecticut, returned Dec. 10, 1950.

PEITZMEIER, J. 1951. Uber die Wirkung der Trockenheit auf die Vogelwelt. Vogelwelt, **72**: 111–117.—The extreme droughts in central Europe in 1947 and 1949 affected bird populations in many ways: increases or decreases of certain species, shift of habitat or food, and changes of date of migration. The effects are not nearly as severe as those of a very cold winter.

PETRIDES, GEORGE A., AND CHARLES R. BRYANT. 1951. An analysis of the 1949–50 fowl cholera epizootic in Texas Panhandle waterfowl. Trans. 16th N. A. Wildl. Conf., pp. 193–216.—About 4,400 waterfowl perished from *Pasteurella multocida*. Deficient rainfall may make for such outbreaks, typically among crowded concentrations of wintering ducks on relatively small and shallow ponds.

PEUS, FR. 1951. Nüchterne Analyse der Massenvermehrung der Misteldrossel (*Turdus viscivorus* L.) in Nordwesteuropa. Bonner Zool. Beitr., **2** (1–2): 55–82.

PFEIFER, S. 1951. Gruppenbalz oder Frühlingsversammlungen des Eichelhähers? Vogelwelt, **72**: 12–14.—Screaming parties of European Jays in spring are analyzed and interpreted as part of the courtship. The display appears to be precisely like that of the Blue Jay.

PHILLIPS, W. W. A. 1951. Nests and eggs of Ceylon birds (Zosteropidae, Nectariniidae and Pittidae). Ceylon Journ. Sci. (sec. B. Zool.), **24** (3): 145–163, 6 pls.—Full notes on nidification, etc., of two species of white-eyes, three of sunbirds, and three of flower-peckers. The pitta is not yet certainly known to breed in Ceylon.

PHELPS, WILLIAM H., AND WILLIAM H. PHELPS, JR. 1951. Four new Venezuelan birds. Proc. Biol. Soc. Wash., **64**: 65-72, 1 fig. (map).—*Glaucidium brasilianum margaritae* (Boca de Río, at sea level, Isla de Margarita, Nueva Esparta); *Chamaeza campanisona huachamacarii* (Cerro Huachamacare, 650 meters, Territorio Amazonas); *Phylloscartes chapmani duidae* (Cerro Duida, 1980 meters, Territorio

Amazonas); *Phylloscartes nigrifrons maguirei* (Cerro Paraque, 1500 meters, Territorio Amazonas).

PITELKA, FRANK A. 1951. Ecologic overlap and interspecific strife in breeding populations of Anna and Allen hummingbirds. Ecology, **32** (4): 641–661.—A five-year study indicated that due to interspecific competition *Calypte anna* maintained a population density at 80% of the maximum possible in the 125 acres, while for *Selasphorus sasin* this was only 48%.

PITELKA, FRANK A. 1951. Nomenclature of the Hooded Jay: a correction. Condor, **53** (6): 300.—*Cyanolyca mitrata* becomes *C. cucullata*.

PITELKA, FRANK A. 1951. The tyrannid Aechmolophus mexicanus in Guerrero. Condor, **53** (6): 300.—Heretofore known only from two specimens, a third is reported from Chilpancingo.

POST, GEORGE. 1951. Effects of toxaphene or chlordane on certain game birds. Journ. Wildl. Manag., **15** (4): 381–386.—Total game bird mortality in plots baited with these insecticides was 23 per cent; in control plots, 10 per cent.

PRESTWICH, ARTHUR A. 1951. Records of parrots bred in captivity. Part IV. (Ring-necks and Kings). (A. A. Prestwich, London), pp. 122–180.

PRZYGODDA, W. 1951. Feldmausbekämpfung und Vogelwelt. Vogelwelt, **72**: 106–111.—The effect on birds of feeding field mice killed by various poisons.

RABELER, W. 1951. Systematik der Vogelgemeinschaften im Hinblick auf Biozonötik und Pflanzensoziologie. Ornith. Abhl., **9**: 3–10.—The relation of birds to plant associations.

REQUATE, H. 1951. Uber Brutausfall durch den Befall mit der Schmeissfliege *Lucilia sericata* Meigen bei einigen Seevogelarten. Vogelwelt, **72**: 33–34.—Larvae of this fly entered freshly-pecked eggs, delayed hatching, and killed the young within a day after hatching.

RINGLEBEN, H. 1951. Aus dem Leben des Mittelsägers (*Mergus serrator* L.). Part 1. Vogelwelt, **72**: 43–50, 84–87, 119–128.—A detailed life history of the Red-breasted Merganser. Social life before and during breeding season and a description of the various types of displays, nest location, incubation, and hatching.

RIPLEY, S. DILLON. 1951. Birds collected and noted round Dhahran, Saudi Arabia, and Bahrein Island. Postilla [Yale Peabody Mus. Nat. Hist.], No. **9**: 1–11.—Notes on twenty-odd forms, of which three are described as new: *Ammomanes deserti insularis* (Bahrein Island); *Pycnonotus leucotis dactylus* (Dammam, near Dhahran, Saudi Arabia); *Prinia gracilis anguste* [sic] (Bahrein Island). *Ammomanes deserti insularis* Ripley, May 10, 1951, has 12 days' priority over *Ammomanes deserti faenorum* Meinertzhagen, May 22, 1951.—H. G. DEIGNAN.

RIPLEY, S. DILLON. 1951. Three birds from the mountains of Muscat. Postilla [Yale Peabody Mus. Nat. Hist.], No. **10**: 1–2.—Remarks on a dove, a lark, and a pipit. The lark is described as new: *Galerida cristata thomsi* (Seik, Jebel Akhdar, Muscat).

RIPLEY, S. DILLON. 1951. Migrants and introduced species in the Palau Archipelago. Condor, **53** (6): 299–300.—Seven species reported on.

RITTINGHAUS, H. 1951. Der Star als Nahrungsschmarotzer der Zwergseeschwalbe (*Sterna albifrons*). Vogelwarte, **16**: 15–17.—Starlings tore fish out of bill of attacking Least Terns.

RITTINGHAUS, H. 1951. Uber das Verhalten koloniebrütender Seevögel gegenüber Raubvögeln und anderen Vogelarten. Vogelwelt, **72**: 149–152.—Observations on the behavior of terns, plovers, and shelducks towards gulls, crows, hawks, and other predatory species.

ROLLIN, NOBLE. 1951. A central electro-photographic recorder and comparator. Dawn Song and all Day, **1** (5): 45–47.—Brief description of use of a "robot bird watcher" which works on basis of translating activities into light which is recorded on micro-film. The machine has immense possibilities.

ROSENE, WALTER. 1951. Breeding bird populations of upland field borders. Journ. Wildl. Manag., **15** (4): 434–436.—Field borders planted to *Lespedeza sericea* averaged 11.7–11.9 breeding pairs per 1000 feet in contrast to 9.5–9.8 for control areas.

SAUNDERS, GEORGE B. 1951. A new White-winged Dove from Guatemala. Proc. Biol. Soc. Wash., **64**: 83–87.—*Zenaida asiatica alticola* (near Patzún, altitude about 6900 feet, Department of Chimaltenango).

SAVILE, D. B. O. 1951. The Ring-billed Gull at Ottawa, Ontario, and its field recognition. Can. Field-Nat., **65** (3): 109–112, 1 table.—Emphasizes similarities to and distinctions from Herring Gull at various ages.

SAVILE, D. B. O. 1951. Bird observations at Chesterfield Inlet, Keewatin, in 1950. Can. Field-Nat., **65** (4): 145–157, 2 tables.—Annotated list covering 48 species, plus sections on migration (some southbound in spring at this station), population density (breeding census), and phenology.

SCHEER, G. 1951. Ueber die zeitliche Differenz zwischen Erwachen und Gesangsbeginn. Volgewarte, **16**: 13–15, diagram.—European Robins begin to sing about 3 minutes after awakening; European Blackbirds 5–6 minutes; Chaffinches 15–20 minutes. It is incorrect to equate awakening with the beginning of singing.

SCHILLER, EVERETT L. 1951. The cestoda of Anseriformes of the North Central States. Amer. Midl. Nat., **46** (2): 444–461.—List of tapeworms found in 184 birds examined. As many as 1,680 worms of six different species may be found in a single host bird. The occurrence of many cestodes is not limited to a single species of birds; the same form of the parasite may occur in several host birds. It seems that a balance between host and parasite is frequently reached, without serious harm to the bird.—H. I. FISHER.

SELANDER, ROBERT K., AND SHERMAN J. PREECE, JR. 1951. Cock roosts of Nighthawks. Condor, **53** (6): 302–303.—Observations on *Chordeiles minor* indicate that gregarious roosting assemblages of males are of common occurrence and that such behavior may be normal for breeding as well as non-breeding individuals.

SICK, H. 1951. Das Ei von *Nyctibius grandis* (Gmelin) und Bemerkungen über andere Tagschläfer-Eier. Vogelwelt, **72**: 40–43.—A description of the eggs and nesting sites of *Nyctibius griseus* and *grandis*.

SIMMONS, K. E. L. 1951. The autumn flight-reactions of House Sparrows, swallows and other passerines. Brit. Birds, **44** (11): 369–372.—Intra- and interspecific chasings by *Passer domesticus* and *Hirundo rustica* are apparently a "type of exaggerated social response."

SIMMONS, K. E. L. 1951. Raptor migration in the Suez area: Autumn 1949–Spring 1950. Ibis, **93** (3): 402–406, 1 text-fig.

SIMMONS, K. E. L. 1951. Interspecific territorialism. Ibis, **93** (3): 407–413.—The concept of interspecific territorialism is defined as "a territory holder of one species exhibits persistent aggressive behaviour to an intruding bird of a second species, showing to it some, if not all of the reactions usually forthcoming in intraspecific encounters." Examples are cited, based on the author's field experience in the region of the Suez Canal. The conclusion is that "interspecific territorialism is apparently one of the means evolved to eliminate the effect of competition between closely allied species with a similar ecology."—J. L. PETERS.

SIMMONS, K. E. L., AND A. G. HURRELL. 1951. Nile Valley Sunbirds in the Suez Canal Zone. Ibis, **93** (3): 468–469.

SKEAD, C. J. 1951. A study of the Hadedah Ibis. Hagedashia h. hagedash. Ibis, **93** (3): 360–382, 1 pl.—A study of its biology, conducted in the Albany district, Cape Province.

SPENCER, DAVID L., URBAN C. NELSON, AND WINSTON A. ELKINS. 1951. America's greatest goose-brant nesting area. Trans. 16th N. A. Wildl. Conf., pp. 290–295.—The Yukon-Kuskokwim Delta is a key area for Cackling Geese and Black Brant. Early establishment of a national refuge is recommended.

SPRINGER, PAUL F., AND JOHN R. WEBSTER. 1951. Biological effects of DDT applications on tidal salt marshes. Trans. 16th N. A. Wildl. Conf., pp. 383–397.—Dosages of 0.2–1.6 lbs. per acre had little effect on birds. Swallows and gulls moved off after spraying.

STABLER, ROBERT M., AND CARLTON M. HERMAN. 1951. Upper digestive tract trichomoniasis in Mourning Doves and other birds. Trans. 16th N. A. Wildl. Conf., pp. 145–163.—Infections of *Trichomonas gallinae* reached epizootic proportions during the summer of 1950 in the Southeastern States.

STEWART, ROBERT E. 1951. Clapper Rail populations of the Middle Atlantic States. Trans. 16th N. A. Wildl. Conf., pp. 421–430.—In Virginia, 71 nests averaged 8.38 ± 0.18 per acre, their density being directly correlated with the acreage of edge. In 47 acres of *Spartina alterniflora*, they averaged 2.5 per acre; 80 per cent were within 15 feet of tidal creeks. Hatching success in 1950 was very high, about 90 per cent. Of 198 banded, 4 per cent were shot by hunters.—J. J. HICKEY.

TANDAN, BHUP KISHORE. 1951. Mallophagan parasities from Indian birds. Part 1. Ann. and Mag. Nat. Hist., ser. 12, **4** (44): 802–813, 13 figs.

TAIBEL, ALULAH M. 1951. La Tortora dal collare orientale—*Streptopelia decaocto decaocto* (Friv.)—avvistata anche nel Polesine. Accertata nidificazione a Rovigo. Riv. Ital. Ornit., **21** (4): 137–150.

TAKASHIMA, HARUO. 1950. Gruidae of Japan and its adjacent territories. Tori, **13**(60): 5–9.—Brief discussion and listing of status of cranes in the area. In Japanese with English summary.

TANTZEN, R. 1951. Ergebnisse der Storchforschung im Land Oldenburg 1949 und in den angrenzenden Gebieten. Ornith. Abhl., **9**: 11–28.—In normal years 90 per cent of the storks return to northwest Germany before the end of April. In 1949 two-thirds arrived in May. Most of these birds failed to nest. Only 67 young were raised in Oldenburg, as against 196 in 1948, and 716 in 1939. Conditions in the winter quarters seem more responsible for these fluctuations than do those in the breeding area. Birds from this area have been recovered from both the southeastern and southwestern migration routes.—E. MAYR.

TEIDOFF, EDGAR. 1951. Zur Ökologie, Biologie und Psychologie des Haselhuhns (*Tetrastes bonasia*). Bonner Zool. Beitr., **2** (1–2): 99–108.

TERRILL, LEWIS MCI. 1951. Shore bird migration at Montreal. Can. Field-Nat., **65** (3): 87–98.—Extensively annotated list; arrival and departure dates.

THOMPSON, ST. CLAIR. 1951. The southeastern cooperative dove study. Trans. 16th N. A. Wildl. Conf., pp. 296–306.—Monthly population trends, plot and roadside counts, and band-recovery rates are compared. Rural mail carriers' counts ran within the narrow limits of 11.8–24.7 doves per 100 miles, while biologists' road counts ran 4.7–63.1. Young birds can be aged by means of dropped primaries (the 9th is dropped at 130 days). The percentage of immatures among

birds bagged has varied widely, 35–89 per cent, but causes for these variations are not explained.—J. J. HICKEY.

THOMSON, A. L., AND E. P. LEACH. 1951. Report on bird-ringing for 1950. Brit. Birds, **44** (9): 289–310.—76,106 birds were ringed, 33,994 being nestlings. Sixteen pages are devoted to a "Selected List of Recoveries."

TIMMERMANN, G. 1951. Aus meinem isländischen Tagebuch 1949–1950. Vogelwelt, **72**: 34–40, 77–82.—Life history notes on the Icelandic population of many arctic species of birds.

TORNIELLI, ANNIBALE. 1951. Comportamento di migratori nei riguardi di un pozzo metanifero in fiamme. Riv. Ital. Ornit., **21** (4): 151–162, 1 fig.

TURČEK, F. 1950. O vztahu sojky (Garrulus glandarius L.) k obnove dubu (Quercus sp.) (The Continental Jay in relation to the oak and its distribution.) Lesnická Práce, **29** (9–12): 385–396.—English summary. About 25 years ago jays began to underplant a 100-year-old monoculture of Scotch pine on 5412 hectares in West-Slovakia. Now about half the forest is underplanted and in some stands the oak undergrowth is a dense canopy. Average underplanting is about 50% of artificial planting. A map of the Eastern Hemisphere shows the close correspondence between the ranges of the oak and the jay.—M. M. NICE.

VAN BEMMEL, A. C. V., AND K. H. VOOUS. 1951. On the birds of the islands of Muna and Buton, S. E. Celebes. Treubia, **21** (1): 27–104, 1 fig.—An annotated report on material from these two islands in the museums of Amsterdam and Bogor, and in the private collection of J. G. van Marle. Three forms are described as new: *Aceros cassidix brevirostris* van Bemmel (Labasa, Muna Island); *Accipiter rhodogaster butonensis* Voous (Buton Island); *Treron pompadora dehaani* Voous (Buton Island).—H. G. DEIGNAN.

VAN DEN AKKER, JOHN B., AND VANEZ T. WILSON. 1951. Public hunting on the Bear River Migratory Bird Refuge, Utah. Journ. Wildl. Manag., **15** (4): 367–381.—Hunting results (1932–1948) are analyzed. Green-winged Teals and Pintails were the species most often taken. Sex ratio on 53,000 shot in 5 years was 79 males to 100 females. The age ratio in 1947 was 0.68 young per adult.—J. J. HICKEY.

VAN DEN BRINK, J. N. 1951. De turkse tortel, *Streptopelia d. decaocto* Friv., thans ook broedvogel in Nederland. Limosa, **24** (1–2): 10–11.—The first breeding record for the species in Holland.

VAURIE, CHARLES. 1951. A new race of *Artomyias fulginosa* from Southern Nigeria. Bull. Brit. Orn. Club, **76** (6): 37–38.—*Artomyias fuliginosa chapini*, new subspecies.

VAURIE, CHARLES. 1951. A new species of flycatcher from Mindanao, Philippine Islands. Amer. Mus. Novit., No. **1543**: 1–4.—*Muscicapa crypta* new species, from Mt. McKinley, Mindanao; related to *M. hyperythra*, *M. bonthaina*, and *M. rufigula*. Known from three specimens.

VERHEYEN, RENÉ. 1950. Sur la portée pratique due "Cline" en ornithologie systématique. Inst. Roy. Sci. Nat. Belgique, **26** (60): 1–10.

VERHEYEN, R. 1951. De Watervogels van België (Met Uitzondering der Eendvogels en der Steltlopers). (Koninklijk Belgisch Inst. Natuurwet., Brussels), pp. 1–173, 65 figs.—Using the term "waterfowl" in its broadest sense, the author undertakes, in the first 35 pages, to discuss the variability of this group and to emphasize the rôle of the environment in effecting many of the superficial resemblances between sub-groups. In this discussion are included similarities in structure, behavior, and ecology. On pages 36–45 is a key to some of the water-

fowl of Belgium. Following this is the systematic account for each species. Included here one may find: a brief synonymy; description of plumages by sexes and ages; breeding behavior; description of anatomical features; and distribution. For certain forms the information is detailed—the species of *Podiceps, Phalacrocorax, Sterna,* and *Larus,* for example.

The ducks, phalaropes, and gruiform birds are not included, having been considered in previous papers. The paper would have been more valuable to those unacquainted with the literature had there been a more complete listing of already-published studies.—H. I. FISHER.

VESELOVSKY, Z. 1951. Postembryonální vývoj kachny chocholaté (Nyroca fuligula L.). Sylvia, **13** (1): 1–19.—This study of the postembryonic development of the Tufted Duck is concerned primarily with plumage changes shown in 15 birds raised in captivity from the eggs. Changes in color of iris, sex differences at hatching, growth of bill, differential growth of bill and limbs, weights, voice, and behavior are noted in some detail. English summary.—H. I. FISHER.

VIERECK, H. v. 1951. Ueber die Ursachen fuer die Abnahme der Ringelgans (*Branta bernicla*) in den Winterquartieren. Vogelwarte, **16**: 18–22.—European Brant, badly decimated by the eelgrass disease, are still decreasing. Since eelgrass is also beginning to recover in European waters, unfavorable conditions in the breeding quarters may be responsible for the continued decline.—E. MAYR.

VOROBIEV, K. A. 1951. Novaya forma indiiskoi kukushki—*Cuculus micropterus ognevi* subsp. nova. Doklady Akademii Nauk SSSR [Reports Acad. Sci. U.S.S.R.], [new ser., 19] **77** (3): 511–512.—The type (from Guberovo, mid-course of the Ussuri) and three specimens from Amur-land differ from two Indian specimens of *C. m. micropterus* by greater length of wing and bill (wing length 200–213 mm., against 188–192 mm.). The new form ranges from Amur-land and the frontiers of Ussuri-land through Manchuria into Korea (southward limits uncertain).—H. G. DEIGNAN.

WENDLAND, V. 1951. Zwanzigjährige Beobachtungen über den Schreiadler *Aquila pomarina*. Vogelwelt, **72**: 4–11.—A life history of the Spotted Eagle. Two territories were occupied for 20 years consecutively. Nest, eggs, incubation period, death of second young, feeding, prey, habitat, and population density are discussed.

WESTERNHAGEN, W. v. 1951. Raubvogelzug an der Ostseeküste. Ornith. Mitt., **3**: 7–11.—Description of magnitude and direction of hawk migration along the shores of the western Baltic.

WETMORE, ALEXANDER. 1951. Observations on the genera of swans. Journ. Wash. Acad. Sci., **41** (10): 338–340.—After a study of the comparative osteology, the author places the seven living swans in three genera: *Chenopis, Cygnus,* and *Olor* (the last divided into the subgenera *Olor* and *Clangocygnus*). All generic names so far used for the group are allocated.—H. G. DEIGNAN.

WHITE, C. M. N. 1951. Systematic notes on African birds. Ibis, **93** (3): 460–465.—Two races of *Hagadashia hagedash* are recognized definitely, and a third tentatively. The races of *Butorides striatus* from Madagascar and the Seychelles appear to have been derived from African mainland stock; those from Mauritius, Réunion, Rodriguez, Assumption, Diego Garcia and the Comoro Islands show more affinities with the race of southern Asia (*B. s. javanicus*). It is proposed to lump the ralline genera *Limnocorax, Porzana, Crecopsis,* and *Aenigmatolimnas* with *Crex. Pterocles namaqua ngami* is not separable from *P. namaqua; P. burchelli makarikari* is valid; *P. bicinctus chobiensis* is not regarded as recognizable. *Treron australis clayi* White, 1943 becomes *T. a. salvadorii* (Dubois) 1897, and *T. a.*

salvadorii of authors, not of Dubois, becomes *T. a. granviki* Grote 1924. The correct subspecific name of the South African form of *Anthus richardi* is *rufuloides* Roberts. It is believed that the types of *Bradornis benguellensis* Bocage are wrongly labelled and did not come from Benguella. *Lanius collaris congicus* Reichenow (1902) is considered a synonym of *L. c. capelli* Bocage (1879).—J. L. PETERS.

WILLIAMS, JOHN G. 1951. Notes on *Scepomycter winifredae* and *Cinnyris loveridgei*. Ibis, **93** (3): 469–470.—Notes on plumage and habits of these two species based on specimens taken and observations made in the Uluguru Mts., Tanganyika.

YAMASHINA, Y. 1950. Duck hybridization by artificial insemination. Tori, **13** (60): 1–5, 2 figs.—Description of Onishi's method of securing sperm and inseminating female; of significance in obtaining crosses to check interspecies fertility.

YEAGER, LEE R., WAYNE W. SANDFORT, AND L. JACK LYON. 1951. Some problems of Pheasant management on irrigated land. Trans. 16th N. A. Wildl. Conf., pp. 351–367. "Despite a mortality of 69.0 per cent in [313] nests, 24.9 per cent in [792] chicks, and 19.6 per cent in [296] adults . . . the late-summer populations showed 255 to 311 per cent increases over the breeding populations during the 3-year period of 1948–50." Crop harvest activities destroyed 35 per cent of all nests, 8 per cent of all chicks, and 28 per cent of all nesting hens. Weather was second in importance as a mortality factor.—J. J. HICKEY.

ZIMMER, JOHN T. 1951. Studies of Peruvian Birds. No. 61. The genera *Aglaeactis, Lafresnaya, Pterophanes, Boissonneaua, Heliangelus, Eriocnemis, Haplophaedia, Ocreatus,* and *Lesbia*. Amer. Mus. Novit., No. **1540**: 1–55.—Taxonomic revisions, including remarks on hybridization. New races are: *Aglaeactis castelnaudii regalis* from Rumicruz, Dept. Pasco, Peru; *A. cupripennis cajabambae* from Cajabamba, Peru; *Lafresnaya lafresnayi orestes* from San Pedro, south of Chachapoyas, Peru; *Pterophanes cyanopterus caeruleus* from Paramo Guamues, Nariño, Colombia; *Heliangelus amethysticollis decolor* from Rumicruz, Dept. Pasco, Peru; *Eriocnemis luciani marcapatae* from Marcapata, southeastern Peru; and *Ocreatus underwoodii ambiguus* from Salento, western Quindio Andes, Colombia.

OBITUARIES

WALTER ALLEN ANGELL, an Honorary Life Associate, elected to the American Ornithologists' Union in 1901, died at Smithfield, Rhode Island, on February 5, 1950. He was born in Johnston, R. I., September 5, 1868. After attending the Johnston Public Schools, he became a taxidermist and furrier and developed into a well-rounded naturalist. He also manufactured Riker mounts for use in the study of insects. His collection of rare butterflies was destroyed completely in the hurricane of 1938. He also specialized in the raising of dahlias and gladiolas. Aside from a collection of bird skins, domestic and foreign, he had one of the best collections of the eggs of the birds of New England, found for the most part by himself.—A. W. SCHORGER.

FRANK WESTON BENSON, an Associate of the American Ornithologists' Union, elected in 1920, died at Salem, Massachusetts, November 14, 1951, at the age of 89. He was born at Salem on March 24, 1862. After studying at the Boston Museum of Fine Arts, he went to the Julian Academy in Paris where he was a pupil of Boulanger and Lefebre. His initial reputation as an artist was gained in oil. Probably

the most widely known of his paintings are the seven panels that he did for the Library of Congress.

He turned wholeheartedly to etchings and drypoints in 1912 and soon acquired the reputation of being the most original and virile of American etchers. His strength lay in the delineation of birds, particularly shorebirds and waterfowl with their settings of beach and marsh. His output was prodigious. Of the 310 plates that appeared between 1912 and 1930, nearly two-thirds have birds as the major or minor subject.

Benson was an enthusiastic sportsman. His self-portrait, "The Gunner," shows a face so kind that the dead birds at his side seem only an essential sacrifice to art. It was only by many hours of patient observation in a blind that he attained that mastery of every motion of waterfowl in flight and the characteristic poses of the shorebirds. In his work the marsh grasses sway and the water ripples as in life. His etchings of Yellow-legs are so successful that the viewer unconsciously expects them to nod at any moment.

The artist was a member of the: Guild of Boston Artists; National Association of Portrait Painters; Brooklyn Society of Etchers; Chicago Society of Etchers; Ten American Painters; National Institute of Arts and Letters; National Academy of Design; and Academician. Awards in the form of medals and monetary prizes were many. Exhibits were held at home and abroad, and today his works form part of the permanent collections of most of the large galleries of our country.—A. W. SCHORGER.

SIDNEY CHASE, an Associate of the American Ornithologists' Union since 1904, died at Nantucket, Massachusetts, March 21, 1932, in his 85th year. He was born in Nantucket in 1847. He married Ella Merrihew of Fairhaven and, after her death in 1909, retired from business and returned to Nantucket.

Chase was much interested in birds. He is said to have contributed his observations on birds to various ornithological journals but apparently did not publish any notes in 'The Auk'.—T. S. PALMER.

ELIZABETH RAND COX, an Associate of the American Ornithologists' Union, elected in 1949, died in Plainfield, New Jersey, on November 9, 1950. She was born in Perth Amboy, N. J., on October 24, 1908. After graduating from Smith College in 1930, she took special work at the University of New Mexico and Rutgers University. Her interest in birds began in 1942 and, through a natural gift in art and music combined with a retentive memory, she soon became familiar with the habits and notes of the birds of her region. Frequent drives to Bay Head, N. J., permitted her to become acquainted with the birds of marsh and beach. She was skilled in ceramics, and her models of the Kingfisher and Bob-white won first prizes in the Plainfield Art Society. Miss Cox was avid in acquiring knowledge for its own sake, and she had a broad interest in politics, education, and the Unitarian Church. She was known for her generosity, humor, and pleasing personality.—A. W. SCHORGER.

HERMANN GROTE, elected a Corresponding Fellow of the American Ornithologists' Union in 1923, died in Berlin, Germany, on August 12, 1951. He was born on July 7, 1882. Grote went to German East Africa as director of a sisal plantation and in 1909 (Ornith. Monatsber., 17: 21–24, 103–104, 147–149) began the publication of a series of notes on the birds of German East Africa that continued until 1913. While serving in the German Army in World War I, he was made prisoner by the Russians. Taking up the study of their language, he performed invaluable service to the western nations by translating into German many Russian reports on ornithology.

Grote retained a deep interest in the African avifauna and by a close study of the collections in Berlin he was able to recognize and name a considerable number of new forms. In 1930, in the "Mitteilungen" of the Berlin Museum, he published a very valuable paper on the Palearctic migrants visiting tropical and southern Africa, 199 species in all, outlining their winter ranges, and giving the dates for their movements. This was followed in 1931 and 1937 by two supplementary articles on the same subject.

After World War II Grote again took up work at the Berlin Museum, but his health failed. Those who knew him personally were impressed with his great friendliness and deep devotion to systematic ornithology.—JAMES P. CHAPIN.

EDWARD KING HAMMOND, an Associate of the American Ornithologists' Union, elected in 1937, died of a heart attack, September 29, 1950, at his home in Chicago. He was born in Morgan Park, now a part of Chicago, Illinois, October 25, 1885, and graduated in mechanical engineering from the American Institute of Technology in 1909. He was a bachelor and lived, in the region where he was born, with his sister, Violet F. Hammond, who was his only surviving near relative. She died November 19, 1951.

Hammond was a former editor of the magazine 'Machinery,' and he was the western manager of this magazine from 1921 to the time of his retirement in June, 1947. He was elected a member of the Kennicott Club of Chicago in 1935. His collection of eggs and nests of birds was given to the Chicago Academy of Sciences.—R. M. STRONG.

HAROLD HERRICK of Lawrence, Long Island, New York, a Life Associate of the American Ornithologists' Union, died May 27, 1933, in his 80th year. He was born in New York City, November 26, 1853, the son of Jonathan K. and Elizabeth (Telles) Herrick. On November 26, 1878, he married Annie T. Lawrence. In 1872 he entered the insurance business in New York and from 1896 to 1917 served as president of the Niagara Fire Insurance Company. Herrick was elected an Associate of the A.O.U. in 1905. His contributions to 'The Auk' were limited to a few brief notes on game birds in the vicinity of New York and on the Monroe Marshes of Lake Erie where, for a number of years, he was accustomed to hunt waterfowl.—T. S. PALMER

JOHN SOUTHGATE YEATON HOYT, one of the most promising young ornithologists at Cornell, died at Memorial Hospital, New York City, on June 1, 1951. He was born January 13, 1913, in Baltimore, the son of Dr. W. D. Hoyt and Margaret Y. Hoyt who moved in 1915 to Washington and Lee University where Dr. Hoyt became head of the Department of Biology.

"South," as he was always called by his many friends, took his B.S. degree from Washington and Lee in 1938, and then came to Cornell to study ornithology under Dr. Arthur A. Allen. His main graduate problem was the life history of the Pileated Woodpecker, out of which grew his M.S. and Ph.D. dissertations and numerous publications about the growth and molt of this interesting species.

During the war Dr. Hoyt served as a medical technician in the Army Medical Corps, first at Stark General Hospital in Charleston, S. C., and later in the Kennedy General Hospital at Memphis, Tennessee. His wife, Sarah Foresman Hoyt, to whom he was married in 1942, was employed in similar work with civilian status. During these years Dr. and Mrs. Hoyt were active in bird-banding, leading field trips, and even helping to organize bird and general natural history societies. Perhaps the work they enjoyed most was their Directorship of Natural History at Cold

Spring Harbor Biological Laboratory, Long Island, for they spent their summers there from 1941 through 1950, except for the period when they were doing war work.

After the war, Dr. and Mrs. Hoyt moved to the small village of Etna, near Ithaca, where until December 1, 1950, Dr. Hoyt served as an assistant in the Laboratory of Ornithology. Here his work as a preparator, instructor, extension lecturer, and radio program leader was most helpful. His fortitude and cheerfulness during his long illness never lapsed, and he is greatly missed by the University staff, his radio audiences, his Boy Scouts, and droves of Ithaca children.

Dr. Hoyt became an Associate of the American Ornithologists' Union in 1935 and was a member of numerous other scientific societies.

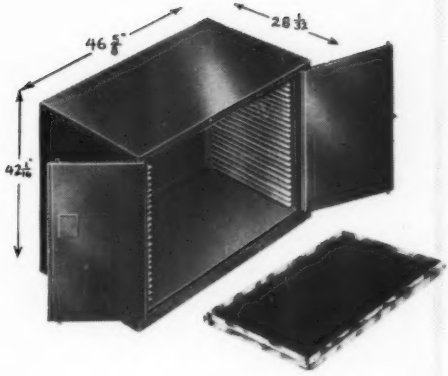
He is survived by two brothers and his wife, who is continuing some of her husband's work.—ELSA G. ALLEN.

ROBERT OWEN MERRIMAN, an Associate of the American Ornithologists' Union, elected in 1920, died at Kingston, Ontario, Canada, October 12, 1934, at the age of 39. He was born in Hamilton, Ontario, December 21, 1895. Bodily infirmities prevented his attendance at the annual meetings of the Union, and he was present at only one, the meeting in Quebec in 1932, when he presented a brief note on 'The Behavior of a Land Bird (Junco) at Sea.' Apparently his only contribution to 'The Auk' was an obituary notice of Edwin Beaupre, published in 1930.—T. S. PALMER.

OSCAR RUDOLPH NEUMANN, a Corresponding Fellow of the American Ornithologists' Union, died in Chicago, Illinois, May 17, 1946, in the 79th year of his age. He was born in Berlin, Germany, September 3, 1867, the son of a wealthy family, and at an early age developed an interest in natural history and travel. In November, 1892, at the age of 25, he started from Tanga, German East Africa, and proceeded across northern Tanganyika Territory, southern Uganda, and Kenya Colony, around Lake Victoria, to Kwa Mtesa in Uganda. The collections made on this trip were presented to the Berlin Museum and his report, under the title of 'Beitrage zur Vogelfauna von Ost- und Central-Afrika,' was published in the 'Journal für Ornithologie' for 1898–1900. In 1899 he accompanied Baron von Erlanger on an expedition to Somaliland and southern Ethiopia. From Zeila, on the Gulf of Aden, the party traveled to Addis Ababa, Ethiopia, and Neumann went on alone to Shoa to find a new route to the Sudan. His account of this expedition appeared in 'The Geographical Journal' for 1902; his birds were acquired by the Tring Museum and his report on the 1300 birds collected appeared in the 'Journal für Ornithologie' for 1904–1906, under the title 'Vögel von Schoa und Sud-Aethiopien.'

In 1908, Neumann, who had lost most of his fortune by unfortunate investments, was offered a position in the Tring Museum, but this plan failed a few months later when Lord Rothschild was in financial difficulties. Neumann then became a stockbroker in Berlin and continued in this business for 25 years, when it was terminated by the Hitler regime. After the outbreak of World War II life in Berlin became unsafe and Neumann, with the aid of a friend, made his way to Cuba in 1941 and then to Chicago where he became a curator in the Field Museum, now the Chicago Natural History Museum.

He was elected a member of the British Ornithologists' Union in 1897, but for financial reasons was obliged to resign in 1910. He was elected a Corresponding Fellow of the American Ornithologists' Union in 1928 and a Foreign Member of the B.O.U. in 1929. He was unmarried.—T. S. PALMER.



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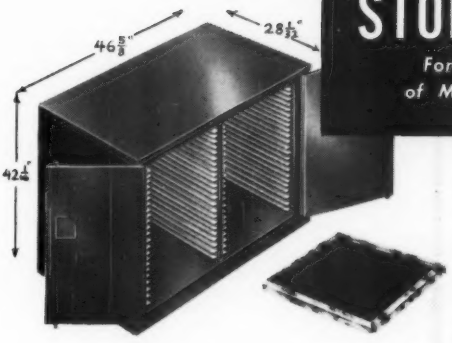

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